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SPATIAL OVERLAP AND HABITAT ASSOCIATIONS OF BARRED OWLS AND GREAT HORNED OWLS IN SOUTHERN NEW JERSEY

KIM J. LAIDIG[1] AND DAVID S. DOBKIN[2]

Department of Biology, Rutgers University, Camden, NJ 08102 U.S.A.

ABSTRACT.—Barred owls (*Strix varia*) are closely associated with relatively undisturbed mature forest, in contrast to great horned owls (*Bubo virginianus*) which are characteristically associated with highly fragmented landscapes of forests and fields. The two species are potential competitors, and great horned owls may prey upon barred owls. We assessed the relative abundance and distribution of both species in areas of known barred owl abundance by using taped playback of conspecific vocalizations. Estimated relative abundances of the two owls were virtually identical, and estimated home ranges overlapped extensively between the two species, although our data suggest that temporal partitioning may have reduced actual overlap. Barred owls were associated with cedar swamp-pitch pine lowland habitat and depended on mature hardwood swamp forest for nest sites, but suitable nesting habitat was extremely limited and occurred only in small patches. Forest fragmentation is likely responsible for the extraordinary degree of spatial overlap found between the two species in southern New Jersey and poses a continuing threat to the integrity of the region's barred owl population.

KEY WORDS: *Barred owl; Bubo virginianus; great horned owl; spatial overlap;* Strix varia; *temporal overlap; vocal responsiveness.*

Sobreposición espacial y asociaciones de hábitat de *Strix varia* y *Bubo virginianus* en el sur de New Jersey

RESUMEN.—*Strix varia* está estrechamente asociada a bosques maduros relativamente no perturbados, en contraste a *Bubo virginianus* característicamente asociado a paisajes de bosques y campos altamente fragmentados. Ambas especies son potencialmente competidoras, incluso *B. virginianus* puede predar sobre *S. varia*. Medimos la abundancia relativa y distribución de ambas especies en áreas de conocidas abundancias de *S. varia*, realizando "playbacks" con vocalizaciones conespecíficas. Las abundancias relativas estimadas para los dos búhos fueron virtualmente idénticas. Los rangos de hogar estimados se sobreponían extensamente entre ambas especies, aunque nuestros datos sugieren que la partición temporal puede haber reducido la actual sobreposición. *Strix varia* estaba asociado a hábitat de tierras bajas pantanosas y con pendiente, dependía de bosques leñosos maduros para ubicar sus nidos. Pero este propicio tipo de hábitat era extremadamente escaso y se daba sólo en pequeños parches. Probablemente, el fenómeno de la fragmentación de bosques es el responsable del extraordinario grado de sobreposición espacial entre ambas especies de búhos, en el sur de New Jersey y plantea una continua amenaza a la integridad de la población de *S. varia* de la región.

[Traducción de Ivan Lazo]

The barred owl (*Strix varia*) is widely distributed throughout North America east of the Rockies and

across Canada to British Columbia (Clark et al. 1987, Johnsgard 1988). In recent years, the species has expanded its westernmost range into northwestern Montana and northern Idaho, southeastern Alaska, much of western British Columbia, and south through the Cascades of Washington, Oregon, and northern California (Johnsgard 1988, Verner et al. 1992).

[1] Present address: The Pinelands Commission, P.O. Box 7, New Lisbon, NJ 08064 U.S.A.

[2] Present address: High Desert Ecological Research Institute, 15 S.W. Colorado Avenue, Suite 300, Bend, OR 97702 U.S.A.

The broad geographic range of barred owls belies a distribution that is often highly localized because of their close association with mature and old-growth forest (Johnsgard 1988), and the owl's relative intolerance of anthropogenic disturbance (Bosakowski et al. 1987, Bosakowski 1989). For example, barred owls in New Jersey have been extirpated from many parts of the state (New Jersey Department of Environmental Protection 1985), and presently occur in substantive numbers only in the extreme northwest (Bosakowski et al. 1987, 1989a) and south (Sutton and Sutton 1985, Sutton 1988)—the only regions that still provide extensive tracts of relatively undisturbed broad-leaved or mixed forest.

Successful management of small, disjunct barred owl populations requires a clear understanding of population distribution and habitat dependency. Although portions of the area inhabited by the southern New Jersey population are protected from development within the Pinelands National Reserve, much of southern New Jersey remains subject to intense development pressure (Collins and Russell 1988). In addition, forest fragmentation as a result of clearcutting, firewood harvest, and deer management (as elsewhere in eastern North America) routinely create openings within contiguous forest. Such forestry practices bring the more disturbance-tolerant great horned owl (*Bubo virginianus*), with its regionally expanding population (Harwood 1988, Bosakowski et al. 1989b), into contact with the more reclusive, forest-dwelling barred owl (Bosakowski et al. 1987, 1989a,b). Great horned owls pose a potential threat to barred owls as predators of both adults and young (Bent 1938, Grant 1966, Fuller 1979, Bosakowski et al. 1989c), and as potential competitors with considerable prey overlap (Johnsgard 1988, Bosakowski and Smith 1992).

The objectives of our study were to (1) assess the relative abundances and distributions of barred owls and great horned owls in southern New Jersey, and (2) examine habitat associations of the two species.

METHODS AND STUDY AREAS

Barred owls and great horned owls were sampled separately during seven survey periods from May 1988 through May 1989, using tape playback of conspecific vocalizations. This technique is particularly efficient for detecting barred owls, which are reliably and highly responsive to tape playback or vocal imitation (McGarigal and Fraser 1984, 1985, Bosakowski 1987).

Six survey routes traversing areas with the greatest potential numbers of barred owls were selected based on previous roadside surveys conducted in southern New Jersey (Sutton and Sutton 1985, Sutton 1988). Survey routes were located in the state's three southernmost counties (Cape May, Cumberland, and Atlantic), and focused on Belleplain State Forest and adjacent state wildlife management areas, Great Cedar Swamp, Bear Swamp, and Mays Landing. Each survey route consisted of 10 broadcast stations at 1-km intervals. Taped territorial vocalizations (Peterson 1983) were broadcast at each station using a Uher 4000 Report Monitor set at full volume. Each broadcast consisted of six repetitions of a 10-sec set of calls followed by 50 sec of silence. The tape recorder speaker was rotated 180 degrees between each 10-sec set of vocalizations to provide broadcast into the forest on both sides of the roadway. Completion of each broadcast was followed by a 10-min response time. Barred owl broadcasts consisted of a single individual followed by a pair of owls emitting the "standard" vocalization. Great horned owl broadcasts consisted of an individual emitting the six- to eight-syllable call that is typical of this species.

Survey periods were separated by 6–8 wk; within each period, surveys for each species on a route were separated by 1–2 wk. Sampling order for each species was alternated between survey periods. Surveys were conducted between sundown and sunrise when wind speed was low and precipitation negligible. At each broadcast station, presence/absence data were collected based on vocal responses or visual contacts. This survey technique assumes that an owl's response indicates intrusion by a conspecific into its breeding territory or home range (Fuller and Mosher 1981).

To simplify habitat quantification, we approximated annual home ranges of owls (Nicholls and Fuller 1987) by circular plots superimposed on U.S. Fish and Wildlife Service National Wetland Inventory (NWI) vegetation maps, with each broadcast station as the center point. Our goal was not to precisely delimit owl home ranges or to determine centers of activity, but rather to characterize conservatively the relative habitat composition within areas likely utilized by owls. To facilitate comparisons, we used circular plots representing a home range of 369 ha for each species, based on radio-telemetry tracking studies conducted in other parts of their ranges (Nicholls and Warner 1972, Fuller 1979, Petersen 1979, Elody and Sloan 1985). Although 369 ha approaches the documented upper limit for barred owl home ranges, we selected this value because (1) it approximated the mid-range of great horned owl home-range sizes, (2) within species, avian home ranges tend to be larger in habitats characterized by low biological productivity (as found on the New Jersey coastal plain [Woodwell 1979]), and (3) roads generally were located in uplands, hence larger plots were necessary to counter underestimation of wetland habitat types. Circular plots of this size spaced at 1-km intervals ensured sampling of habitats at spatial scales appropriate to known movement distances by these species.

As noted by Bosakowski (1987), responses less than 2 km apart should be evaluated cautiously to consider whether owls belong to the same or adjacent territories. We conservatively assessed the spatial and temporal distribution of owl responses to taped vocalizations in combination with mapped estimated home ranges to determine the maximum number and distribution of owl home ranges on each survey route. (Sonagraphic analysis of taped vocal responses for individual identification of barred owls confirmed that at least some individuals responded from adjacent stations [Dobkin and Laidig unpubl. data].) We placed broadcast stations at relatively

Table 1. Number of stations ($N = 10$ per route) yielding barred owl/great horned owl responses on each survey, and estimated total number of home ranges for each species on each survey route in southern New Jersey, May 1988 to May 1989.

ROUTE	SURVEY MONTH/YEAR							ESTIMATED HOME RANGES
	5/88	6/88	8/88	11/88	1/89	3/89	5/89	
Belleplain	2/1	0/1	2/3	4/2	2/0	2/1	3/1	3/3
Buckshutem	2/0	1/2	4/1	0/0	0/4	1/2	4/0	3/3
Cedar Swamp	1/0	0/0	1/0	0/1	1/3	0/2	1/0	1/1
Mays Landing	1/0	1/3	1/0	0/1	0/0	0/0	0/0	1/1
Port Elizabeth	3/1	0/4	1/2	0/0	2/1	0/3	2/0	2/2
Steelmantown	a	1/0	3/1	3/2	1/1	0/0	3/1	3/2
Total								13/12

a Not surveyed.

short, 1-km intervals to increase the probability of owl detections that might otherwise be missed due to (1) variation in owl location within its home range at the time of tape broadcast, and (2) variation in effective transmission distance of broadcasts and detectability of owl vocal responses.

Habitats at each broadcast station were determined from the NWI maps, which delimit 19 habitat types in the vicinity of the survey routes. We condensed these habitat types to five categories: (1) upland oak-pine forest (UP) dominated by relatively short, small-diameter trees, (2) hardwood-mixed hardwood swamp (HMS) usually dominated by large deciduous overstory trees and frequently with dense understories, (3) cedar swamp-pitch pine lowland (CSPP) consisting of Atlantic white cedar (*Chamaecyparis thyoides*) or pitch pine (*Pinus rigida*), respectively; lowland pine understories usually were quite dense, (4) shrub-scrub (SS) of low woody growth that often resulted from clearcut timber harvest, fire, or abandoned cranberry bog succession, and (5) emergent-open water wetlands (EMOW) of shallow ponds or marshes with a notable absence of trees and shrubs. More detailed accounts of floristic composition are provided by McCormick (1979). Coverage by each habitat within the plots was quantified with a Numonics electronic planimeter.

We used nonparametric statistics (Siegel and Castellan 1988) to avoid problems of nonnormality and heteroscedas-

ticity in the data. Owl responses were analyzed by chi-square and binomial tests. Habitat differences between stations with and without owls were examined by Mann-Whitney U-tests. Frequencies of owl occurrence in relation to percent coverage of different habitats were assessed with Spearman rank correlations, but these tests were not performed on the shrub-scrub and emergent-open water habitat types to avoid distortion and possible spurious correlations due to the large number of zeros in the data set (Ludwig and Reynolds 1988).

RESULTS

Relative Abundances and Vocal Responsiveness. We obtained a total of 53 barred owl and 44 great horned owl responses (Table 1). Routes that were most productive for barred owls also were the most productive for great horned owls. Conversely, routes that produced the fewest responses from barred owls also were the least productive for great horned owls (Table 1). Barred owls and great horned owls each responded at 31 of 60 stations surveyed (Table 2), with each species responding exclusively at 16 of 31 stations. Hence, over the duration of the entire study, neither

Table 2. Spatial overlap of barred owls (B) and great horned owls (G) based on responses[a] to playback of tape-recorded conspecific vocalizations along survey routes in southern New Jersey, May 1988 to May 1989.

ROUTE	BROADCAST STATION NUMBER									
	1	2	3	4	5	6	7	8	9	10
Belleplain	BG	–G	–G	BG	B–	–G	BG	B–	BG	BG
Buckshutem	BG	BG	BG	B–	B–	BG	BG	B–	––	–G
Cedar Swamp	––	–G	––	B–	BG	–G	––	––	––	––
Mays Landing	B–	–G	–G	–G	––	––	––	––	B–	––
Port Elizabeth	–G	B–	BG	B–	––	B–	–G	–G	–G	–G
Steelmantown	B–	B–	BG	BG	B–	B–	B–	–G	BG	–G

[a] B and G indicate at least one response at a station over the course of the entire study period; – indicates no response.

Table 3. Percent coverage of habitat types in 369-ha circular plots centered on owl survey stations ($N = 60$) in southern New Jersey.

Habitat Type[a]	Mean (SD)	Minimum	Maximum
UP	71.6 (19.0)	16.8	97.6
HMS	22.8 (16.9)	0.9	79.5
CSPP	2.0 (2.1)	0.0	13.1
SS	2.1 (3.2)	0.0	12.9
EMOW	1.5 (4.8)	0.0	32.6

[a] UP = upland oak-pine forest, HMS = deciduous hardwood-mixed hardwood swamp, CSPP = cedar swamp-pitch pine lowland, SS = shrub-scrub, EMOW = emergent-open water.

Table 4. Spearman rank correlation coefficients for barred owl and great horned owl occurrence with percent coverage by habitat type in estimated home ranges centered on each survey station ($N = 60$) along routes in southern New Jersey, May 1988 to May 1989.

Habitat Type[a]	Barred Owl	Great Horned Owl
UP	−0.14	0.00
HMS	0.21	−0.08
CSPP	0.30[b]	−0.08

[a] UP = upland oak-pine forest, HMS = deciduous hardwood-mixed hardwood swamp, CSPP = cedar swamp-pitch pine lowland
[b] $P = 0.05$.

positive nor negative interspecific association could be detected among stations. Of the 15 stations where both species responded, however, only four instances occurred in which both species responded from the same station within the same survey period (even though surveys for each species were separated by 1-2 wk). This suggests a possible avoidance or spatiotemporal partitioning of areas between the two species where home ranges overlapped extensively ($z = 1.56$, $P = 0.06$).

Viewed over the course of the entire study, adjacent stations frequently yielded responses from single individuals, but most occurred on different survey dates and were evoked in response only to playback at the nearest station. Hence, we view many of these as responses from the same individual. A conservative interpretation of the response data combined with mapping of estimated home ranges results in remarkably similar estimates of home range numbers for each species on each survey route (Table 1), for a total of 13 barred owl and 12 great horned owl home ranges.

Neither species exhibited seasonal differences in responsiveness to taped vocalizations in comparisons between breeding (March to June) and nonbreeding seasons (barred owls, $\chi^2 = 0.13$, df = 1, $P > 0.35$; great horned owls, $\chi^2 = 0.49$, df = 1, $P > 0.20$), or between spring/summer (March to August) and fall/winter (barred owls, $\chi^2 = 0.42$, df = 1, $P > 0.25$; great horned owls, $\chi^2 = 0.32$, df = 1, $P > 0.25$). We recorded the most barred owl responses in May and August, the fewest responses in March and June, and intermediate levels in the winter months (Table 1). Great horned owls responded in relatively uniform numbers across all months surveyed, except for a marked reduction in responsiveness in May surveys (Table 1).

Habitat Associations. Nearly 95% of the total habitat across the 60 stations consisted of upland oak-pine forest and mixed hardwood swamp (Table 3), although the latter comprised less than 25% of the total habitat. However, the percent coverage by each habitat type ranged widely among individual stations (Table 3).

Barred owls were associated positively ($r_s = 0.30$, $P = 0.05$, Table 4) with cedar swamp-pitch pine lowland habitat, but no other significant relationships were found in testing either frequency of owl occurrence (Table 4) or absolute owl occurrence (all tests $P > 0.10$) in relation to percent coverage of habitat types.

DISCUSSION

Relative Abundances and Vocal Responsiveness. Our estimate of barred owl home ranges for all of the survey routes combined is considerably smaller than the numbers reported by Sutton (1988) in his survey of some of these same routes. Our estimates represent a more conservative approach based on survey data in combination with mapping of estimated home ranges over time, and supplemented with vocalization analyses. Sutton (1988) viewed responses from adjacent stations at different survey times as distinct individuals. We considered responses clustered around several adjacent broadcast stations as representing a single pair of birds unless vocalization analyses indicated otherwise. Even allowing for differences in estimation between the two surveys, our results indicate that fewer barred owls occur in southern New Jersey than assumed previously (Sutton 1988).

Other studies that examined habitat overlap between barred and great horned owls generally found distinct habitat separation, with overlap occurring only along

forest margins or where open fields and woodlands were interspersed (Fuller 1979, McGarigal and Fraser 1984, Bosakowski et al. 1989a). We found virtually complete overlap of occupied areas, with only two of 13 estimated barred owl home ranges not extensively overlapped by estimated great horned owl ranges. We infer that the extraordinary degree of spatial overlap demonstrated in our study (1) results from the small-scale, but pervasive fragmentation created by narrow, forest-dividing corridors (Rich et al. 1994), logging, and deliberate ecotonal development for deer management in southern New Jersey forests, and (2) reflects the patchy distribution of mature hardwood and cedar swamp woodlands relative to the extensive oak-pine forest (Forman 1979).

Although spatial overlap was extensive, our data suggest that temporal partitioning may have reduced actual overlap of the two species, as demonstrated by Fuller (1979) with several instances of radio-tagged barred owls that exhibited apparent spatial avoidance behavior in response to great horned owls. Fuller (1979) found that while some annual home ranges of the two species overlapped considerably, very little home range overlap was evident when examined on a weekly basis. Similarly, although 16 stations yielded both species in our study, few overlaps were noted within individual survey periods.

Other studies have reported distinct seasonal variability in barred owl responsiveness to taped playback of vocalizations (Bosakowski 1987). In northern New Jersey, Bosakowski et al. (1987) found barred owl responsiveness to be greatest in the breeding season from March to June, with relatively few responses outside of these months. Smith (1978) recorded higher barred owl response rates in Connecticut in late spring (May to July), and Elody (1983) found high response rates in northern Michigan in summer months.

Incubation by barred owls in New Jersey occurs in March and early April with most egg dates falling between 17 and 29 March (Johnsgard 1988). Barred owl incubation requires 28–33 d and fledging averages 42 d posthatching (Ehrlich et al. 1988). Hence, we found maximum responsiveness during the nestling and early dispersal periods, and found minimal responsiveness during incubation and early fledging periods. This pattern is consistent with very low calling rates recorded during incubation in western Maryland (Devereux and Mosher 1984). Overall, the data suggest that maximum responsiveness occurs during specific portions of the annual cycle (which happen progressively later at higher latitudes), a pattern that can

be obscured by combining responsiveness data on a seasonal basis.

Marked seasonality in responsiveness to taped playback reportedly also characterizes great horned owls, which were noted as most responsive from December through March (Emlen 1973, Smith et al. 1987), but we found no evidence of seasonality. The only apparent deviation from relative uniformity across all months surveyed was the marked decrease seen in May surveys of both years, which corresponds to the beginning of the fledgling period for great horned owls in New Jersey (Bosakowski et al. 1989c), and is consistent with low responsiveness by barred owls during their early fledgling period.

Habitat Associations. Barred owls usually nest in the interior of contiguous forests with mature and decadent trees of sufficient size to provide cavities for nest sites (Dunstan and Sample 1972, Elody 1983, Allen 1987), preferably in stands with trees >51 cm dbh (Devereux and Mosher 1984). Of the habitats available in our study area, only mature hardwood swamps provided trees that were suitable for nest sites. The only old-growth forests in southern New Jersey are hardwood swamps that escaped logging by virtue of their relative inaccessibility. The high commercial value of Atlantic white cedar resulted in essentially complete (and repeated) harvest of cedar stands over the past 300 yr (Collins et al. 1988).

We believe that the association between barred owls and cedar swamp-pitch pine lowlands (which comprised only 2% of the total mapped area) indicates the importance of this habitat for roosting and foraging. Cedar stands provide camouflage and shelter as roost sites (Applegate 1975, Fuller 1979), especially when deciduous trees are leafless, and likely provide thermal refugia in summer (Havens 1979). Cedar swamps also support substantial populations of voles and shrews (Craig and Dobkin 1993)—the primary prey of barred owls in the region (Rusling 1951, Devereux and Mosher 1984, Bosakowski et al. 1987).

Not surprisingly, great horned owls were not associated with any particular habitat in our study, which is consistent with the view that this species is a habitat generalist (Fuller 1979, Petersen 1979, McGarigal and Fraser 1984, Bosakowski et al. 1989a) across the spectrum of forest habitats found in southern New Jersey.

Increased forest fragmentation as a result of habitat manipulation to increase deer populations (creation of "wildlife openings"), logging operations, and the proliferation of utility rights-of-way (Rich et al. 1994) will continue to create habitat conditions that are likely to

benefit great horned owls, but negatively affect barred owls. Thus, the barred owl population in southern New Jersey cannot be considered secure. At the very least, land management activities should not be undertaken that will further diminish suitable barred owl habitat in the region.

LITERATURE CITED

ALLEN, A.W. 1987. Habitat suitability index models: barred owl. USDI Fish Wildl. Serv. Biol. Rep. 82(10.143).

APPLEGATE, R.D. 1975. Co-roosting of barred owls and common grackles. Bird-Banding 46:169-170.

BENT, A.C. 1938. Life histories of North American birds of prey: Part 2. U.S. Natl. Mus. Bull. 170, Washington, DC U.S.A.

BOSAKOWSKI, T. 1987. Census of barred owls and spotted owls. Pages 307-308 in R.W. Nero, R.J. Clark, R.J. Knapton and R.H. Hamre [EDS.], Biology and conservation of northern forest owls. USDA For. Serv. Gen. Tech. Rep. RM-142, Fort Collins, CO U.S.A.

————. 1989. Barred owl. Pages 114-120 in B.G. Pendleton [ED.], Proceedings northeast raptor management symposium and workshop. Natl. Wildl. Fed., Washington, DC U.S.A.

———— AND D.G. SMITH. 1992. Comparative diets of sympatric nesting raptors in the eastern deciduous forest biome. Can. J. Zool. 70:984-992.

————, J. BENZINGER AND R. SPEISER. 1989a. Forest owl populations of the Pequannock Watershed. Records of New Jersey Birds 15:2-8.

————, R. KANE AND D.G. SMITH. 1989b. Decline of the long-eared owl in New Jersey. Wilson Bull. 101:481-485.

————, R. SPEISER AND J. BENZINGER. 1987. Distribution, density, and habitat relationships of the barred owl in northern New Jersey. Pages 135-143 in R.W. Nero, R.J. Clark, R.J. Knapton and R.H. Hamre [EDS.], Biology and conservation of northern forest owls. USDA For. Serv. Gen. Tech. Rep. RM-142, Fort Collins, CO U.S.A.

————, ———— AND D.G. SMITH. 1989c. Nesting ecology of forest-dwelling great horned owls, Bubo virginianus, in the eastern deciduous forest biome. Can. Field-Nat. 103: 65-69.

CLARK, R.J., D.G. SMITH AND L. KELSO. 1987. Distributional status and literature of northern forest owls. Pages 47-55 in R.W. Nero, R.J. Clark, R.J. Knapton and R.H. Hamre [EDS.], Biology and conservation of northern forest owls. USDA For. Serv. Gen. Tech. Rep. RM-142, Fort Collins, CO U.S.A.

COLLINS, B.R. AND E.W.B. RUSSELL [EDS.]. 1988. Protecting the New Jersey Pinelands: a new direction in land-use management. Rutgers Univ. Press, New Brunswick, NJ U.S.A.

————, N.F. GOOD AND R.E. GOOD. 1988. The landscape of the New Jersey Pine Barrens. Pages 3-33 in B.R. Collins and E.W.B. Russell [EDS.], Protecting the New Jersey Pinelands: a new direction in land-use management. Rutgers Univ. Press, New Brunswick, NJ U.S.A

CRAIG, L.J. AND D.S. DOBKIN. 1993. Community dynamics of small mammals in mature and logged Atlantic white cedar swamps of the New Jersey Pine Barrens. New York State Mus. Bull. No. 487, Albany, NY U.S.A.

DEVEREUX, J.G. AND J.A. MOSHER. 1984. Breeding ecology of barred owls in the central Appalachians. Raptor Res. 18:49-58.

DUNSTAN, T.C. AND S.D. SAMPLE. 1972. Biology of barred owls in Minnesota. Loon 44:111-115.

EHRLICH, P.R., D.S. DOBKIN AND D. WHEYE. 1988. The birder's handbook: a field guide to the natural history of North American birds. Simon & Schuster Inc., New York, NY U.S.A.

ELODY, B.J. 1983. Techniques for capturing, marking, monitoring and habitat analysis for the barred owl in the Upper Peninsula of Michigan. M.S. thesis, Michigan Tech. Univ., Houghton, MI U.S.A.

———— AND N.F. SLOAN. 1985. Movements and habitat use of barred owls in the Huron Mountains of Marquette County, Michigan, as determined by radiotelemetry. Jack-Pine Warbler 63:3-8.

EMLEN, J.T., JR. 1973. Vocal stimulation in the great horned owl. Condor 75:126-127.

FORMAN, R.T.T. [ED.]. 1979. Pine barrens: ecosystem and landscape. Academic Press, New York, NY U.S.A.

FULLER, M.R. 1979. Spatiotemporal ecology of four sympatric raptor species. Ph.D. dissertation, Univ. Minnesota, Minneapolis, MN U.S.A.

———— AND J.A. MOSHER. 1981. Methods of detecting and counting raptors: a review. Pages 235-246 in C.J. Ralph and J.M. Scott [EDS.], Estimating numbers of terrestrial birds. Stud. Avian Biol. No. 6.

GRANT, J. 1966. The barred owl in British Columbia. Murrelet 47:39-45.

HARWOOD, M. 1988. Research results: raptors and their prey. Hawk Mountain News 70:25-30.

HAVENS, A.V. 1979. Climate and microclimate of the New Jersey Pine Barrens. Pages 113-131 in R.T.T. Forman [ED.], Pine barrens: ecosystem and landscape. Academic Press, New York, NY U.S.A.

JOHNSGARD, P.A. 1988. North American owls. Smithsonian Inst. Press, Washington, DC U.S.A.

LUDWIG, J.A. AND J.F. REYNOLDS. 1988. Statistical ecology: a primer on methods and computing. John Wiley & Sons, New York, NY U.S.A.

McCORMICK, J. 1979. The vegetation of the New Jersey Pine Barrens. Pages 229–243 in R.T.T. Forman [ED.], Pine barrens: ecosystem and landscape. Academic Press, New York, NY U.S.A.

McGARIGAL, K. AND J.D. FRASER. 1984. The effect of forest stand age on owl distribution in southwestern Virginia. J. Wildl. Manage. 48:1393–1398.

————— AND —————. 1985. Barred owl responses to recorded vocalizations. Condor 87:552–553.

NEW JERSEY DEPARTMENT OF ENVIRONMENTAL PROTECTION. 1985. Endangered and threatened wildlife in New Jersey. Endangered and Nongame Species Program, Div. Fish, Game, and Wildl., Trenton, NJ U.S.A.

NICHOLLS, T.H., AND M.R. FULLER. 1987. Territorial aspects of barred owl home range and behavior in Minnesota. Pages 121–128 in R.W. Nero, R.J. Clark, R.J. Knapton and R.H. Hamre [EDS.], Biology and conservation of northern forest owls. USDA For. Serv. Gen. Tech. Rep. RM-142, Fort Collins, CO U.S.A.

————— AND D.W. WARNER. 1972. Barred owl habitat use as determined by radiotelemetry. J. Wildl. Manage. 36:213–224.

PETERSEN, L. 1979. Ecology of great horned owls and red-tailed hawks in southeastern Wisconsin. Wisconsin Dept. Nat. Res. Tech. Bull. No. 111, Madison, WI U.S.A.

PETERSON, R.T. 1983. A field guide to bird songs of eastern and central North America (sound recordings). Houghton Mifflin Co., Boston, MA U.S.A.

RICH, A.C., D.S. DOBKIN AND L.J. NILES. 1994. Defining forest fragmentation by corridor width: the influence of narrow forest-dividing corridors on forest-nesting birds in southern New Jersey. Cons. Biol. 8:1109–1121.

RUSLING, W.J. 1951. Food habits of New Jersey owls. Proc. Linn. Soc. N.Y. 58-62:38–45.

SIEGEL, S. AND N.J. CASTELLAN. 1988. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., New York, NY U.S.A.

SMITH, C.F. 1978. Distributional ecology of barred and great horned owls in relation to human distribution. M.S. thesis, Univ. Connecticut, Storrs, CT U.S.A.

SMITH, D.G., A. DEVINE, AND D. WALSH. 1987. Censusing screech owls in southern Connecticut. Pages 255–267 in R.W. Nero, R.J. Clark, R.J. Knapton and R.H. Hamre [EDS.], Biology and conservation of northern forest owls. USDA For. Serv. Gen. Tech. Rep. RM-142, Fort Collins, CO U.S.A.

SUTTON, C. 1988. Barred owl survey of South Jersey, 1987 Records of New Jersey Birds 14:2–5.

————— AND P.T. SUTTON. 1985. The status and distribution of barred owl and red-shouldered hawk in southern New Jersey. Cassinia 61:20–29.

VERNER, J., R.J. GUTIERREZ AND G.I. GOULD, JR. 1992. The California spotted owl: general biology and ecological relations. Pages 55–77 in J. Verner, K.S. McKelvey, B.R. Noon, R.J. Gutierrez, G.I. Gould, Jr. and T.W. Beck (Tech. Coord.), The California spotted owl: a technical assessment of its current status. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-133, Albany, CA U.S.A.

WOODWELL, G.M. 1979. Leaky ecosystems: nutrient fluxes and succession in the Pine Barrens vegetation. Pages 333–343 in R.T.T. Forman [ED.], Pine barrens: ecosystem and landscape. Academic Press, New York, NY U.S.A.

PRODUCTIVITY, FOOD HABITS, AND BEHAVIOR OF SWAINSON'S HAWKS BREEDING IN SOUTHEAST COLORADO

DAVID E. ANDERSEN[1]

U.S. Fish and Wildlife Service, Colorado Fish and Wildlife Assistance Office,
730 Simms Street, No. 290, Golden, CO 80401 U.S.A. and Department of Wildlife Ecology,
University of Wisconsin, Madison, WI 53706 U.S.A.

ABSTRACT.—From 1984 through 1988, I studied Swainson's hawk (*Buteo swainsoni*) ecology during the breeding season on the Piñon Canyon Maneuver Site (PCMS) in southeast Colorado. The number of nesting attempts located and monitored annually ranged from four in 1984, to 22 in 1987. Nests used by Swainson's hawks were located predominantly in one-seed juniper (*Juniperus monosperma*) or cotton-wood (*Populus* spp.) trees. Traditional nesting success estimates averaged 0.64 and ranged from 0.42 in 1985 to 1.00 in 1984. Mayfield estimates of nesting success ranged from 0.27 (1988) to 1.00 (1984). Based on prey remains collected at nest sites, food deliveries to nestlings consisted primarily of small birds (50%) and mammals (45%), and diet breadth over the 5-yr study period was high. Minimum-convex-polygon home-range size of radio-marked adults during the late-nestling and post-fledging period averaged 21.2 km² in 1985 and 27.3 km² in 1986, with males exhibiting larger home ranges than females ($P = 0.15$) across years. Compared with other breeding Swainson's hawk populations, breeding area reoccupancy among years on the PCMS was moderately high, home ranges during the late-nestling and post-fledging periods were large, and ground-nesting birds were important in the breeding-season diet.

KEY WORDS: *Buteo swainsoni; Colorado; food habits; home range; reproduction; Swainson's hawk.*

Productividad, hábitos alimentarios y conducta de nidificación de *Buteo swainsoni* en el sureste de Colorado

RESUMEN.—Desde 1984 a 1988, estudié la ecología de *Buteo swainsoni* durante la estación reproductiva en el Piñon Canyon Maneuver Site (PCMS), al sureste de Colorado. El número de nidificaciones localizadas y monitoreadas anualmente van desde cuatro en 1984 a 22 en 1987. Los nidos de *B. swainsoni* se localizaron predominatemente en árboles de las especies *Juniperus monosperma* y *Populus* sp. El éxito tradicional del nido fue estimado en un promedio de 0.64 y con un rango de 0.42 (1984) a 1.00 en 1984. Basado en los restos de presa colectados en los sitios de nidificación, el alimento entregado a los polluelos consistió primariamente en pequeñas aves (50%) y mamíferos (45%); la amplitud de la dieta en un período de cinco años de estudio fue alto. Durante los períodos polluelo-tardío y post-volantón (juvenil), el tamaño del rango de hogar (polígono convexo mínimo) de adultos radio-marcados fue en promedio de 21.2 km² en 1985 y 27.3 km² en 1986; los machos exhibieron mayores rangos de hogar que las hembras ($P = 0.15$) a través de los años. Camparando la reocupación del área de nidificación entre años en el PCMS, con otras poblaciones reproductivas de *B. swainsoni,* fue moderadamente alta; el rango de hogar durante los períodos polludelo-tardío y post-volantón fue extenso y las aves que nidificaron en el suelo fueron importantes elementos de la dieta en la estación reproductiva.

[Traducción de Ivan Lazo]

Swainson's hawks (*Buteo swainsoni*) breed primarily in grassland and other open habitats (Johnsgard 1990, Andersen 1991). Several studies of Swainson's hawk breeding season ecology have been conducted in grassland habitats (Olendorff 1972, Dunkle 1977, Gilmer and Stewart 1984). However, those studies were conducted in areas that contained a significant proportion of habitat that had been converted to crop production (e.g., irrigated meadows [Dunkle 1977], cultivated lands [Olendorff 1972], and pasture and hay fields [Gilmer and Stewart 1984]). Few studies have been conducted in largely unaltered habitats (Schmutz et al. 1980, Bednarz and Hoffman 1988), and none has been conducted in shortgrass prairie habitat lacking significant human disturbances that include crop production.

Recently, concern has been expressed regarding

[1] Current address: Minnesota Cooperative Fish and Wildlife Research Unit, U.S. National Biological Service, Department of Fisheries and Wildlife, University of Minnesota, St. Paul, MN 55108 U.S.A.

the population status of Swainson's hawks in several portions of their breeding range (Littlefield et al. 1984, Woffinden 1986, Janes 1987, Risebrough et al. 1989, Estep and Tersa 1992). The causes of population declines are not clear (Risebrough et al. 1989), although disagreement exists regarding the influence of crop production in grassland ecosystems on Swainson's hawks (Bechard 1983, Gilmer and Stewart 1984, Schmutz 1984, 1987, 1989, Schmutz and Hungle 1989, Bechard et al. 1990). To place current population levels in historical perspective and to understand the potential impact of conversion of grasslands to agricultural cultivation on breeding Swainson's hawks, information from breeding populations in relatively unaltered habitats may be useful. Herein, I describe the nesting ecology of Swainson's hawks in shortgrass prairie habitats in southeast Colorado, where the predominant land use since the late 1880s has been livestock grazing.

STUDY AREA AND METHODS

The study was conducted on the 1040-km² Piñon Canyon Maneuver Site (PCMS) in southeast Colorado (Fig. 1) from 1984 through 1988. Elevation on the PCMS, located adjacent to the northwest rim of the Purgatoire River Canyon in Las Animas County, ranged from 1310–1740 m (U.S. Department of the Army 1980). Topography consisted of broad, moderately sloping uplands bordered by the Purgatoire River Canyon on the southeast, limestone hills on the west, and a basalt hogback on the south. Average annual precipitation on the semi-arid PCMS was 32 cm, but it fluctuated widely from year to year and among sections of the study area (U.S. Department of the Army 1980). Mean monthly temperature ranged from −1° C in January to 23° C in July.

Vegetation on the PCMS was dominated by shortgrass prairie and pinyon (*Pinus edulis*)-juniper (*Juniperus monosperma*) woodland (Costello 1954, Kendeigh 1961). Dominant perennial grass species included blue grama (*Bouteloua gracilis*), sideoats grama (*B. curtipendula*), western wheatgrass (*Agropyron smithii*), galleta (*Hilaria jamesii*), and needle-and-thread (*Stipa comata*). Dominant trees and shrubs included pinyon pine, juniper, cholla (*Opuntia imbricata*), yucca (*Yucca glauca*), fourwing saltbush (*Atriplex canescens*), broom snakeweed (*Gutierrezia sarothrae*), Bigelow sagebrush (*Artemisia bigelovii*), mountain mahogany (*Cercocarpus montanus*), winterfat (*Ceratoides* spp.), and rabbitbrush (*Chrysothamnus* sp.). For a more complete description of vegetation on the PCMS see Shaw and Diersing (1990). Predominant land use on the PCMS since settlement by people of European descent in the 1880s (Friedman 1985, Knight et al. 1989) has been livestock grazing.

I located Swainson's hawk nests by searching potential nesting habitat (e.g., isolated cottonwood [*Populus* spp.] trees and the ecotone between grassland and pinyon-juniper woodland) on foot or horseback, from a vehicle or all-terrain cycle, and from a helicopter. Locations of old
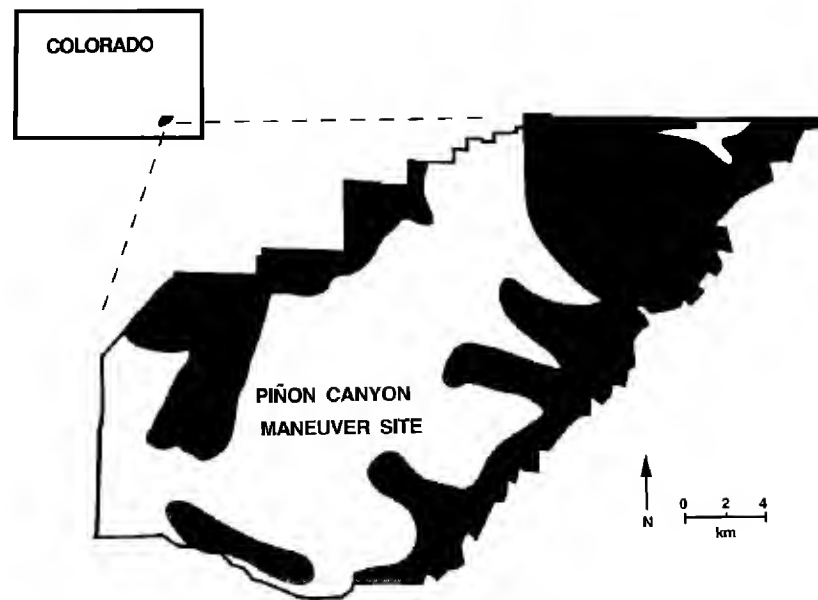

Figure 1. Location of the Piñon Canyon Maneuver Site in southeastern Colorado. Shaded areas represent the approximate extent of pinyon-juniper woodland habitats. Unshaded areas represent shortgrass prairie habitats.

stick nests and observations of Swainson's hawks during the breeding season were plotted on 1:24 000 U.S. Geological Survey topographic maps. Old nests and the immediate vicinity around where adults were sighted were searched for evidence of breeding attempts. Each year I searched the immediate vicinity of all Swainson's hawk nests that had been located in previous years. Nesting attempts and potential nest sites were also identified during productivity surveys conducted from helicopters during June and July for nesting red-tailed (*B. jamaicensis*) and ferruginous hawks (*B. regalis*).

Swainson's hawk territories on the PCMS were defined based on the presence of nesting attempts. Individual nests that were used for nesting in >1 yr were included in the same territory. In addition, different nests between and among years were included in the same territory when the distance between nest sites was smaller than the average minimum distance between nesting attempts among territories from 1984 through 1988 ($N = 6$ territories), or when individuals equipped with radiotransmitters nested at different nests between years ($N = 3$).

Accessible nests were climbed to at least once during the nestling period, except in 1987 and 1988, when only a portion of nests were visited. At each visit, nestlings were weighed and the age of nestlings (days since hatching) was estimated based on fourth primary measurements (Petersen and Thompson 1977, D.E. Andersen unpubl. data) Hatching dates were estimated from nestling age, based on a 34-d incubation period (Bednarz and Hoffman 1988).

Terminology and definitions related to reproduction follow those of Steenhof (1987). A breeding territory was identified when young were raised or eggs were laid, or an adult was observed in incubating posture on a nest. Nesting success rates were calculated using both the Mayfield and traditional methods (Mayfield 1961, 1975, Johnson 1979, Steenhof and Kochert 1982)—I used a 34-d incubation period and a 45-d nestling period (Bednarz and Hoffman 1988) in calculating Mayfield nesting success

Table 1. Number of breeding pairs, nesting success, and productivity of Swainson's hawks on the Piñon Canyon Maneuver Site, Colorado, 1984–88.

YEAR	NUMBER OF PAIRS		NESTING SUCCESS[a]		YOUNG FLEDGED/ BREEDING PAIR	YOUNG FLEDGED/ SUCCESSFUL BREEDING ATTEMPT
	BREEDING	SUCCESSFUL	TRADITIONAL	MAYFIELD		
1984	4	4	1.00 (4)[b]	1.00 (3)	1.75 (4)	1.75 (4)
1985	12	5	0.42 (12)	0.33 (11)	0.75 (12)	1.80 (5)
1986	15	8	0.53 (15)	0.31 (14)	0.93 (15)	1.75 (8)
1987	22	12	0.60 (20)	—	1.00 (18)	1.64 (11)
1988	7	4	0.67 (6)	0.27 (5)	0.83 (6)	1.25 (4)
Total	60	33				
Mean			0.64	0.48	1.05	1.64

[a] Terminology for nesting success is after Steenhof and Kochert (1982) and Steenhof (1987).
[b] Number of nests from which estimate was derived.

estimates. A nesting attempt was classified as successful when young were ≥50% of average fledging age when the status of the nest was last known (based on feather development and behavior) or were observed free-flying in the vicinity of the nest.

At each nest visit, prey remains were removed from the nest for identification and measurement. Prey remains were identified using guides to local fauna (Armstrong 1972, Burt and Grossenheider 1976, Hammerson 1982, National Geographic Society 1983) or by comparison to reference material collected on the PCMS. Diet breadth was calculated using Levins' (1968) formula based on frequencies across years of individual prey species in the diet, following the suggestion of Greene and Jaksić (1983). Pocket gophers (*Thomomys, Geomys*) were combined into a single group without identification to species. Birds not identified to species were excluded from diet-breadth analyses.

In 1985 and 1986, adult Swainson's hawks that were members of breeding pairs were captured using a variation of the technique described by Bloom et al. (1992). Captured birds were fitted with battery-powered, solar-assisted radiotransmitters attached as a backpack (Andersen 1994). Radio-equipped Swainson's hawks were sexed based on observation of relative size and behavior subsequent to capture.

During the period from capture through migration from the study area (approximately mid-September), Swainson's hawks equipped with transmitters were located and followed for 3–4-hr tracking periods, with locations recorded at 0.5 hr intervals (Andersen and Rongstad 1989). Individual birds were tracked in either the morning or the afternoon at approximately 7–10-d intervals systematically through the study period (Andersen and Rongstad 1989). Fixes were obtained by a single observer during a tracking period and were either based on visual observation or triangulation from telemetry signals. Fixes based only on telemetry signals were obtained by a single observer receiving signals from more than two locations in sequence and plotting signal direction on 1:24000 topographic maps. Universal transverse mercator grid coordinates were re-corded from 1:24000 topographic maps of the study area to the nearest 100 m for each radio fix, and the behavior (perched or flying) of the bird and whether the fix was based on visual observation or telemetry signal were noted Minimum convex polygon (MCP) home ranges were calculated for the late-nestling and post-fledging period using the computer program SEAS (J.R. Cary, University of Wisconsin, Madison). All sequential locations were included in MCP analyses (Andersen and Rongstad 1989)

Descriptive statistics, pairwise statistical tests, and analysis of variance (ANOVA) procedures follow those outlined in Snedecor and Cochran (1980). Chi-square tests for independence are after Gibbons (1985).

RESULTS

Reproduction. The number of breeding territories on the PCMS ranged from four in 1984 to 22 in 1987 (Table 1). Traditional nesting success averaged 0.64 (coefficient of variation [c.v.] = 0.34), and the average age of young in the nest at the last time when the nest status was known ranged from 65–80% of fledging age. Mayfield estimates of nesting success averaged 0.48 (c.v. = 0.73). Young fledged per successful breeding attempt averaged 1.64 and exhibited little variation (c.v. = 0.14) among years. Estimated hatching dates were concentrated in mid- to late June, and extended into July in 1984, 1986, and 1988. No differences in hatching dates were evident among years (1-way ANOVA, $F_{3,19} = 0.51$, $P = 0.680$).

A total of 34 territories and 60 nests were identified on the PCMS from 1984 through 1988. Swainson's hawk nests were primarily located in junipers (76% of 60 nests) and cottonwoods (15%), with four of the remaining nests in elms (*Ulmus* sp.) planted

Table 2. Number and frequency of occurrence of prey remains collected at 20 Swainson's hawk nest sites on the Piñon Canyon Maneuver Site, Colorado, 1984–87.

| | YEAR | | | | TOTAL | |
SPECIES	1984	1985	1986	1987	NUMBER	%
Birds						
Western meadowlark (*Sturnella neglecta*)	2	1	1	3	7	11.7
Horned lark (*Eremophila alpestris*)	6	0	0	0	6	10.0
Mourning dove (*Zenaida macroura*)	1	0	0	2	3	5.0
Scaled quail (*Callipepla squamata*)	0	1	0	0	1	1.7
Lark bunting (*Calamospiza melanocorys*)	0	0	0	1	1	1.7
Unidentified birds	1	8	1	2	12	20.0
Total Birds	10	10	2	8	30	50.0
Mammals						
Pocket gophers (Geomyidae)	3	9	9	0	21	35.0
Spotted ground squirrel (*Spermophilus spilosoma*)	1	0	1	0	2	3.3
Ord's kangaroo rat (*Dipodomys ordii*)	0	2	0	0	2	3.3
Desert cottontail (*Sylvilagus audubonii*)	0	1	0	1	2	3.3
Total Mammals	4	12	10	1	27	45.0
Reptiles						
Eastern fence lizard (*Sceloporus undulatus*)	0	0	1	0	1	1.7
Texas horned lizard (*Phrynosoma cornutum*)	0	0	1	0	1	1.7
Unidentified snake	0	0	1	0	1	1.7
Total Reptiles	0	0	3	0	3	5.0
Total	14	22	15	9	60	100.0

as windbreaks, and one in a pinyon pine. When I compared the proportion of territories where different nest structures were used, Swainson's hawks predominantly used territories with junipers (73% of 34 territories) and cottonwoods (12%) as nest sites (2 [6%] additional territories had nests in both junipers and cottonwoods in different years). Nearest-neighbor distances between nests ranged from 3.4 km in 1987 to 9.2 km in 1984, and averaged 5.6 km over the 5-yr study period. On average, nesting attempts were located in territories 55% of the years that they were monitored when including the year that territories were first identified, and 31% of years subsequent to the year they were first identified.

Food Habits. A total of 60 prey remains was collected from 20 nest sites on 12 breeding territories from 1984 through 1987 (Table 2). No prey remains were encountered at nests in 1988. Fifty percent of prey items encountered were birds, 45% were mammals, and the remaining 5% were lizards and snakes. Excluding reptiles ($N = 3$), the relative frequencies of birds and mammals in prey remains were not independent of year ($\chi^2 = 13.41$, df = 3, $P < 0.005$)

and diet breadth for all years combined was relatively high (B = 6.52).

Home Range and Movements. Six Swainson's hawks were captured and fitted with radio transmitters. Two of those individuals returned to the study area the year following capture with functioning radios, and were radiotracked during two breeding seasons. The remaining individuals were tracked during one breeding season (Table 3). Individual hawks were monitored for an average of 6.5 tracking periods per season, resulting in an average of 57 locations per bird. Locations were obtained based on direct visual observation (30.4%), extrapolation from an immediately preceding or subsequent direct visual observation (18.7%), extrapolation within a tracking period where the bird was observed at least once (28.3%) but not immediately preceding or subsequent to the fix, or only on reception of a telemetry signal (22.6%).

Combining MCP estimates from both males and females, home range size averaged 21.3 km² in 1985 and 27.3 km² in 1986 ($t = -0.74$, df = 5, $P = 0.49$). Males ($\bar{x} = 31.7$ km²) tended to have larger home
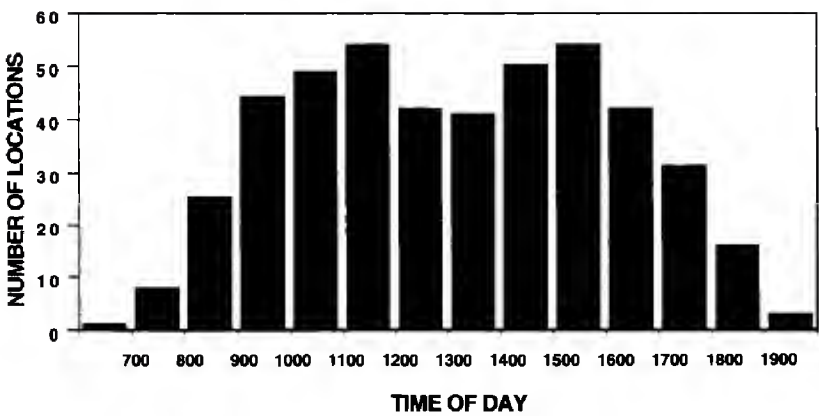
Figure 2. Radio-telemetry locations for six Swainson's hawks captured and monitored in southeastern Colorado from 1986–87 as a function of time of day.

Table 3. Tracking history, behavior, and post-fledging season home range size of adult radio-equipped Swainson's hawks on the Piñon Canyon Maneuver Site, Colorado 1985–86.

YEAR	IDENTIFICATION NUMBER	SEX	NO. OF TRACKING PERIODS	TOTAL NO. OF LOCATIONS	% OF LOCATIONS FLYING	MCP HOME RANGE (km²)
1985	8	F	8	64	78	24.4
	17	M	7	67	87	23.8
	10	F	4	31	84	6.8
	18	M	7	62	92	30.0
1986	8	F	7	69	55	12.1
	10	F	7	63	81	34.2
	26	M	6	52	71	41.3
	30	F	6	52	63	21.7

ranges than females ($\bar{x} = 19.9$ km²), both when MCP area for each breeding season and each year were treated as independent observations ($t = 1.69$, df = 6, $P = 0.15$), and when I calculated an average MCP home range size for the two females that were tracked in both 1985 and 1986 ($t = 2.21$, df = 4, $P = 0.16$).

The proportions of locations obtained in each 1-hr time interval from 0800–1800 H when all locations from all tracking periods were combined, were not distributed significantly differently from random ($\chi^2 = 14.08$, df = 9, $P > 0.05$). Sampling intensity prior to 0800 and after 1800 was not comparable to intensity during that time interval (Fig. 2). During the periods that radio-marked birds were monitored, both males ($\bar{x} = 83\%$ of locations) and females ($\bar{x} = 72\%$ when calculated as independent observations and $\bar{x} = 71\%$ when based on between-year averages), spent the majority of their time flying.

DISCUSSION

Reproduction. Swainson's hawks nesting in shortgrass prairie habitat in southeast Colorado from 1984 through 1988 exhibited moderate nesting success and stable productivity. The number of nesting attempts located annually was highly variable. These results are comparable to descriptions of reproductive parameters from other portions of the breeding range of Swainson's hawks, where the mean number of young fledged per successful nest ranged from 1.19–2.00, and the mean number of young fledged per breeding pair ranged from 1.11–1.85 (Olendorff 1972, Dunkle 1977, Fitzner 1978, Bednarz and Hoffman 1988). As has been noted in other raptors

(e.g., tawny owls [*Strix aluco*; Southern 1970]; great horned owls [*Bubo virginianus*; Rusch et al. 1972, McInvaille and Keith 1974]; ferruginous hawks [Smith et al. 1981]), the most highly variable reproductive parameter for Swainson's hawks on the PCMS appeared to be the proportion of pairs that attempted nesting.

It is not clear from this study, however, whether all territories were occupied annually, even in the absence of a nesting attempt, or whether the PCMS population of Swainson's hawks tracked local prey populations, as has been suggested elsewhere (Schmutz and Hungle 1989). Similar to other temperate-zone raptors, the number of young fledged per successful nesting attempt was relatively stable over the 5-yr period (Newton 1979), suggesting that breeding conditions in territories that fledged young were relatively constant among years, or that successful breeders adjusted to changing conditions. There was no evidence for brood reduction, observed in other areas in response to low prey availability (Bechard 1983).

Food Habits. Based on frequency of prey remains collected at nest sites from 1984 through 1987, Swainson's hawks on the PCMS preyed heavily on ground-nesting birds and small mammals (Table 2). These food habits differ from those reported in most other published studies in that birds comprised a high proportion of the diet, compared to the reported predominance of small and medium-sized mammals

in other locations. In Wyoming, Dunkle (1977) reported that 68% of prey items were small mammals and lagomorphs and in Utah, Smith and Murphy (1973) reported that only 17% of prey items were birds. In North Dakota, Gilmer and Stewart (1984) found that ground squirrels and pocket gophers constituted the majority of prey items of nesting Swainson's hawks. Similarly, Schmutz et al. (1980) reported that prey items of nesting Swainson's hawks in Alberta consisted of 85% mammals, 67% of prey items removed from Swainson's hawk nests in Montana were mammals (Restani 1991), and small mammals were the predominant prey of Swainson's hawks in Washington (Bechard 1983). In Mexico, Thiollay (1981) observed lizards and small rodents as the primary prey species of nesting Swainson's hawks, and in New Mexico, nesting Swainson's hawks preyed predominantly on insects and lagomorphs (Bednarz 1988, Bednarz and Hoffman 1988). In contrast, in California, Swainson's hawks have been observed to include birds as the predominant prey in the breeding-season diet (Estep 1989).

Although sample size (60 items from 20 nest sites over 4 yr) was small, Swainson's hawks on the PCMS appeared to have a relatively broad diet. Diet breadth of Swainson's hawks on the PCMS compares with that of red-tailed hawks in Idaho, the species with the most general diet of three large breeding raptors studied by Steenhof and Kochert (1988). High diet breadth of Swainson's hawks on the PCMS is in large part attributable to high variability in food items collected among years (Table 2).

Home Range and Movements. Estimated home range sizes of adult Swainson's hawks during the late-nestling and post-fledging periods on the PCMS were similar to home ranges reported from other comparable studies. Radio-equipped male Swainson's hawks in Washington exhibited an average home range size of 8.9 km² (Bechard 1982). In California, Estep (1989) observed home ranges averaging 27.6 km² for 12 radio-marked Swainson's hawks during the breeding season. On the PCMS, Swainson's hawks had relatively large home ranges, similar in size to those reported in California, and spent the majority of their time budget flying.

Two potential sources of error in calculating home range size were present in data collected in this study. First, because Swainson's hawks on the PCMS spent the majority of their time flying, estimating fixes precisely, even when birds were observed, was difficult. Second, 22.6% of fixes were obtained via sequential triangulation from the ground by one observer. I was unable to estimate the magnitude of the error associated with either of these two sources. However, neither of these sources of error likely introduced bias into estimates of average home range size of Swainson's hawks on the PCMS. Rather, these sources of error probably increased the variance associated with average home range size estimates, reducing the power of statistical comparisons.

Breeding Season Ecology. Ecology of Swainson's hawks breeding in shortgrass prairie habitat in southeast Colorado may be characterized as intermediate between raptors that are territorial year round, and those that are nomadic and exhibit numerical responses to temporary prey abundance in localized areas. Swainson's hawks return to the breeding grounds after potential competitors for nest sites (e.g., red-tailed and ferruginous hawks and great horned owls) have already initiated nesting. They establish territories that are defended against conspecifics and may defend these territories against other species of raptors (Rothfels and Lein 1983, Janes 1984, Bechard et al. 1990, Restani 1991), or alternatively, nest in association with other raptors (Schmutz et al. 1980, Thurow and White 1983). On the PCMS, late-nestling and post-fledging period home range (and possibly breeding territory) size appears to be relatively large, and there is a moderate rate of breeding territory reoccupancy and high variability in the number of nesting attempts initiated among years. Reproductive success is moderately variable, and productivity of successful nests is relatively high and stable.

This reproductive strategy may in large part be explained in terms of annual variability in prey resources. Prey availability that is unpredictable and highly variable may result in birds establishing or reoccupying territories annually, but only breeding in years in which prey availability is above a minimum threshold (Southern 1970). Above this threshold, nest success may be influenced by density-independent factors (e.g., weather), which cause failure of the nesting attempt rather than reducing brood size. Whether this reproductive strategy was typical of Swainson's hawks across the breeding range prior to extensive human-induced changes in landscape patterns is not clear. However, reproductive ecology of Swainson's hawks on the PCMS can serve as a basis for comparison for other populations of Swainson's hawks in areas where grasslands have in part or in whole been converted to crop production.

LITERATURE CITED

ANDERSEN, D.E. 1991. Management of North American grasslands for raptors. Pages 203–210 in B.A. Giron Pendleton, D.L. Krahe, M.N. LeFranc, Jr., K. Titus, J.C. Bednarz, D.E. Andersen and B.A. Millsap [EDS.], Proceedings of the midwest raptor management symposium and workshop. Natl. Wildl. Fed. Sci. Tech. Ser. No. 15, Washington, DC U.S.A.

———. 1994. Longevity of solar-powered radio-transmitters on buteonine hawks in eastern Colorado. J. Field Ornithol. 65:122–132.

——— AND O.J. RONGSTAD. 1989. Home-range estimates of red-tailed hawks based on independent and systematic relocations. J. Wildl. Manage. 53:802–807.

ARMSTRONG, D.M. 1972. Distribution of mammals in Colorado. Mus. Nat. Hist., Univ. Kansas, Monogr. No. 3.

BECHARD, M.J. 1982. Effect of vegetative cover on foraging site selection by Swainson's hawk. Condor 84: 153–159.

———. 1983. Food supply and the occurrence of brood reduction in Swainson's hawk. Wilson Bull. 95:233–242.

———, R.L. KNIGHT, D.G. SMITH AND R.E. FITZNER. 1990. Nest sites and habitats of sympatric hawks (Buteo spp.) in Washington. J. Field Ornithol. 61:156–170.

BEDNARZ, J.C. 1988. A comparative study of the breeding ecology of Harris' and Swainson's hawks in southeastern New Mexico. Condor 90:311–323.

——— AND S.W. HOFFMAN. 1988. The status of breeding Swainson's hawks in southeastern New Mexico. Pages 253–259 in R.L. Glinski, B.A. Giron Pendleton, M.B. Moss, M.N. LeFranc, Jr., B.A. Millsap and S.W. Hoffman [EDS.], Proceedings of the southwest raptor management symposium and workshop. Natl. Wildl. Fed. Sci. Tech. Ser. No. 11, Washington, DC U.S.A.

BLOOM, P.H., J.L. HENCKEL, E.H. HENCKEL, J.K.

SCHMUTZ, B. WOODBRIDGE, J.R. BRYAN, R.L. ANDERSON, P.J. DETRICH, T.L. MAECHTLE, J.O. MCKINLEY, M.D. MCCRARY, K. TITUS AND P.F. SCHEMPF. 1992. The dho-gaza with great horned owl lure: an analysis of its effectiveness in capturing raptors. J. Raptor Res. 26:167–178.

BURT, W.H. AND R.P. GROSSENHEIDER. 1976. A field guide to the mammals. Houghton Mifflin Co., Boston, MA U.S.A.

COSTELLO, D.F. 1954. Vegetation zones in Colorado. Pages iii–x in H.D. Harrington. Manual of the plants of Colorado. Sage Books, Denver, CO U.S.A.

DUNKLE, S.W. 1977. Swainson's hawks on the Laramie Plains, Wyoming. Auk 94:65–71.

ESTEP, J.A. 1989. Biology, movements, and habitat relationships of the Swainson's hawk in the Central Valley of California, 1986–87. Calif. Dept. Fish and Game, Nongame Bird and Mammal Sec. Rep., Sacramento, CA U.S.A.

——— AND S. TERSA. 1992. Regional conservation planning for the Swainson's hawk (Buteo swainsoni) in the Central Valley of California. Pages 775–789 in D.R. McCullough and R.H. Barrett [EDS.], Wildlife 2001: populations. Jones and Stokes Assoc., Inc., Sacramento, CA U.S.A.

FITZNER, R.E. 1978. The ecology and behavior of the Swainson's hawk (Buteo swainsoni) in southeastern Washington. Ph.D. dissertation, Washington State Univ., Pullman, WA U.S.A.

FRIEDMAN, P.D. 1985. Final report of history and oral history studies of the Fort Carson Piñon Canyon Maneuver Area, Las Animas County, Colorado. Powers Elevation Corp., Denver, CO U.S.A.

GIBBONS, J.D. 1985. Nonparametric methods for quantitative analysis. Am. Sciences Press, Inc., Columbus, OH U.S.A.

GILMER, D.S. AND R.E. STEWART. 1984. Swainson's hawk nesting ecology in North Dakota. Condor 86:12–18.

GREENE, H.W. AND F.M. JAKSIĆ. 1983. Food-niche relationships among sympatric predators: effects of level of prey identification. Oikos 40:151–154.

HAMMERSON, G.A. 1982. Amphibians and reptiles in Colorado. Colo. Div. Wildl. Denver, CO U.S.A.

JANES, S.W. 1984. Influences of territory composition and interspecific competition on red-tailed hawk reproductive success. Ecology 65:862–870.

———. 1987. Status and decline of Swainson's hawks in Oregon: role of habitat and interspecific competition. Oreg. Birds 13:165–179.

JOHNSGARD, P.A. 1990. Hawks, eagles, and falcons of North America: biology and natural history. Smithsonian Inst. Press, Washington, DC U.S.A.

JOHNSON, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651–661.

KENDEIGH, S.C. 1961. Animal ecology. Prentice-Hall, Englewood Cliffs, NJ U.S.A.

KNIGHT, R.L., D.E. ANDERSEN, M.J. BECHARD AND N.V. MARR. 1989. Geographic variation in nest-defence behaviour of the red-tailed hawk *Buteo jamaicensis. Ibis* 131:22–26.

LEVINS, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton, NJ U.S.A.

LITTLEFIELD, C.D., S.P. THOMPSON AND B.D. EHLERS. 1984. History and present status of Swainson's hawks in southeast Oregon. *Raptor Res.* 18:1–5.

MAYFIELD, H. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73:255–261.

———. 1975. Suggestions for calculating nest success. *Wilson Bull.* 87:456–466.

MCINVAILLE, W.B. AND L.B. KEITH. 1974. Predator-prey relations and breeding biology of the great horned owl and red-tailed hawk in central Alberta. *Can. Field-Nat.* 88:1–20.

NATIONAL GEOGRAPHIC SOCIETY. 1983. Field guide to the birds of North America. Natl. Geographic Soc., Washington, DC U.S.A.

NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD U.S.A.

OLENDORFF, R.R. 1972. The large birds of prey of the Pawnee National Grassland: nesting habits and productivity, 1969–1971. Tech. Rep. 151, U.S. Internat. Biome Program, Grassland Biome, Fort Collins, CO U.S.A.

PETERSEN, L.R. AND D.R. THOMPSON. 1977. Aging nestling raptors by 4th primary measurements. *J. Wildl. Manage.* 41:587–590.

RESTANI, M. 1991. Resource partitioning among three *Buteo* species in the Central Valley, Montana. *Condor* 93:1007–1010.

RISEBROUGH, R.W., R.W. SCHLORFF, P.H. BLOOM AND E.E. LITTRELL. 1989. Investigations of the decline of Swainson's hawk populations in California. *J. Raptor Res.* 23:63–71.

ROTHFELS, M. AND M.R. LEIN. 1983. Territoriality in sympatric populations of red-tailed and Swainson's hawks. *Can. J. Zool.* 61:60–64.

RUSCH, D.H., E.C. MESLOW, P.D. DOERR AND L.B. KEITH. 1972. Responses of great horned owl populations to changing prey density. *J. Wildl. Manage.* 36:282–296.

SCHMUTZ, J.K. 1984. Ferruginous and Swainson's hawk abundance and distribution in relation to land use in southeastern Alberta. *J. Wildl. Manage.* 48:1180–1187.

———. 1987. The effect of agriculture on ferruginous and Swainson's hawks. *J. Range Manage.* 40:438–440.

———. 1989. Hawk occupancy of disturbed grasslands in relation to models of habitat selection. *Condor* 91: 362–371.

——— AND D.J. HUNGLE. 1989. Populations of ferruginous and Swainson's hawks increase in synchrony with ground squirrels. *Can. J. Zool.* 67:2596–2601.

———, S.M. SCHMUTZ AND D.A. BOAG. 1980. Coexistence of three species of hawks (*Buteo.* spp.) in the prairie-parkland ecotone. *Can. J. Zoology* 58:1075–1089

SHAW, R.B. AND V.E. DIERSING. 1990. Tracked vehicle impacts on vegetation at the Pinyon Canyon Maneuver Site, Colorado. *J. Environ. Qual.* 19:234–243.

SMITH, D.G. AND J.R. MURPHY. 1973. Breeding ecology of raptorial birds in the eastern Great Basin Desert of Utah. Brigham Young Univ. Biol. Ser. 18:1–76. Provo, UT U.S.A.

———, J.R. MURPHY AND N.D. WOFFINDEN. 1981 Relationships between jackrabbit abundance and ferruginous hawk reproduction. *Condor* 83:52–56.

SNEDECOR, G.W. AND W.G. COCHRAN. 1980. Statistical methods. W.H. Freeman and Co., New York, NY U.S.A.

SOUTHERN, H.N. 1970. The natural control of a population of tawny owls. *J. Zool., Lond.* 162:197–285.

STEENHOF, K. 1987. Assessing raptor reproductive success and productivity. Pages 157–170 *in* B.A. Giron Pendleton, B.A. Millsap, K.W. Cline and D.M. Bird [EDS.], Raptor management techniques manual. Natl. Wildl. Fed. Sci. Tech. Series No. 10, Washington, DC U.S.A.

——— AND M.N. KOCHERT. 1982. An evaluation of methods used to estimate raptor nesting success. *J. Wildl Manage.* 46:885–893.

——— AND ———. 1988. Dietary responses of three raptor species to changing prey densities in a natural environment. *J. Anim. Ecol.* 57:37–48.

THIOLLAY, J. 1981. Ségrégation écologique et pression de prédation de deux buses sympatrique dans un désert mexicain. *Gerfaut* 71:575–610.

THUROW, T.L. AND C.M. WHITE. 1983. Nest site relationship between the ferruginous hawk and Swainson's hawk. *J. Field Ornithol.* 54:401–406.

U.S. DEPARTMENT OF THE ARMY. 1980. Draft: Environmental impact statement for acquisition of training land in Huerfano, Las Animas and Pueblo Counties, Colorado. U.S. Army Corps of Engineers, Omaha District, Omaha, NE U.S.A.

WOFFINDEN, N.D. 1986. Notes on the Swainson's hawk in central Utah: insectivory, premigratory aggregations, and kleptoparasitism. *Great Basin Nat.* 46:302–304.

ECOLOGICAL RELATIONSHIPS BETWEEN NESTING SWAINSON'S AND RED-TAILED HAWKS IN SOUTHEASTERN IDAHO

R.W. Hansen[1] and L.D. Flake
Department of Wildlife and Fisheries Sciences, South Dakota State University, Brookings, SD 57007 U.S.A.

Abstract.—We compared reproductive success, nest site characteristics, and food habits of nesting Swainson's hawks (*Buteo swainsoni*) and red-tailed hawks (*B. jamaicensis*) along the Big Lost River and Birch Creek on the Idaho National Engineering Laboratory, southeastern Idaho, from 1991–93. Productivity was similar between species. Twenty-four red-tailed hawk nests produced 34 fledglings (1.4/attempt) while 17 Swainson's hawk nests produced 21 fledglings (1.2/attempt). Nest trees used by Swainson's hawks were shorter, smaller, and more foliated than those used by red-tailed hawks ($P <$ 0.01). Swainson's hawk nest trees were more foliated than most trees along Birch Creek and the Big Lost River ($P <$ 0.006). Red-tailed hawk nest trees were similar to available deciduous trees (>25% dead), but were taller ($P =$ 0.001). Prey remains and castings at nests (% frequency), indicated that Swainson's hawks preyed more commonly on birds than red-tailed hawks while the latter more commonly captured *Lepus* spp. and Sciuridae; Leporidae, including *Lepus* spp. and *Sylvilagus* spp., made up over 60% of the estimated prey biomass for both species. Riparian vegetation condition, notably the lack of narrowleaf cottonwood (*Populus angustifolia*) survival and regeneration, appeared to be a major factor accounting for changes in hawk distribution on the study area.

Key Words: *food habits; habitat degradation; Idaho; nesting; red-tailed hawk; Swainson's hawk.*

Relaciones ecológicas entre *Buteo swainsoni* y *Buteo jamaicensis* nidificantes en el sureste de Idaho

Resumen.—Entre 1991 y 1993 comparamos éxito reproductivo, características del sitio de nidificación y hábitos alimentarios de *Buteo swainsoni* y *Buteo jamaicensis* a lo largo de Big Lost River y Birch Creek en el Idaho National Engineering Laboratory, al sureste de Idaho. La productividad fue similar entre ambas especies. Veinticuatro nidos de *B. jamaicensis* produjeron 34 volantones (1.4/nido) mientras que 17 nidos de *B. swainsoni* produjeron 21 volantones (1.2/nido). Los árboles utilizados para nidificar por *B. swainsoni* fueron más cortos, más pequeños y con mayor dosel que los utilizados por *B. jamaicensis* ($P <$ 0.01). Los árboles para nidificación de *B. swainsoni* poseían un dosel más denso que la mayoría de los árboles a lo largo de Birch Creek y del Big Lost River ($P <$ 0.006). Lós árboles de nidificación de *B. jamaicensis* eran similares a árboles deciduos (>25% muertos) pero eran más delgados ($P =$ 0.001). Los restos de presas y su distribución en el nido (% de frecuencia), indicaron que *B. swainsoni* predaba más comunmente sobre aves que *B. jamaicensis*, mientras que este último capturaba comunmente *Lepus* spp. y Sciuridae; Leporidae, incluyendo *Lepus* spp. y *Sylvilagus* spp., constituyó sobre el 60% de la biomasa de presas estimada para ambas especies. La condición de la vegetación ribereña parece ser un factor importante en el cambio de distribución de *B. swainsoni* en el área de estudio.

[Traducción de Ivan Lazo]

Availability of nesting habitat can be a limiting factor in raptor communities (Newton 1976). The availability of nesting substrate can be especially important for tree-nesting raptors in regions where trees are scarce (Schmutz 1984). Trees along riparian corridors may concentrate nesting raptors. On

the Idaho National Engineering Laboratory (INEL), trees along the Big Lost River and Birch Creek serve as nesting habitat for several raptor species (Craig 1979, Hansen 1994). Swainson's hawks (*Buteo swainsoni*) have been historically the most common *Buteo* species nesting along riparian corridors on the INEL (Craig 1979). However, red-tailed hawk (*B. jamaicensis*) nesting has increased greatly on the study area since the early 1980s (Craig et al. 1984, Hansen 1994). We measured the nesting habitat, food habits, and productivity of both species to examine the re-

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[1] Present address: Department of Range and Wildife Management, Texas Tech University, Lubbock, TX 79409–2125 U.S.A.

lationships between nesting Swainson's hawks and an expanding red-tailed hawk population.

STUDY AREA AND METHODS

The INEL is a 230 000-ha National Environmental Research Park administered by the United States Department of Energy. It is located on the upper Snake River plain in southeastern Idaho (Fig. 1). Human access is restricted to people conducting site maintenance or field research. Most human-related influences on nesting raptors are indirect.

The climate at the INEL is typical of a cold, semi-arid desert, with temperatures ranging between −42 and 39° C, and precipitation averaging 21 cm annually (Clawson et al. 1989). Vegetation on the INEL is dominated by big sagebrush (*Artemisia tridentata*) communities (McBride et al. 1978). Narrowleaf cottonwoods (*Populus angustifolia*) and western water birch (*Betula occidentalis*) along the Big Lost River and Birch Creek, as well as scattered Utah junipers (*Juniperus osteosperma*) provide the majority of raptor nesting habitat on the INEL. Understory vegetation varies little between the river corridors and sagebrush uplands.

We searched the entire length of the Big Lost River and Birch Creek on the INEL for nesting red-tailed and Swainson's hawks from March through July in 1991, 1992, and 1993. Nest search procedures used on the remainder of the INEL are detailed elsewhere (Hansen 1994). Brief, biweekly visits to nest sites provided us with reproductive data for all nesting hawks. During nest visits, we collected prey remains and pellets to determine food habits. Prey occurrence was determined by counting mandibles and by characteristic body parts such as feathers or scales (Marti 1987). Following fledging or nesting failure, we measured nest-site characteristics. These characteristics included: outside nest diameter, nest and nest substrate heights, diameter at breast height (dbh) of nest trees, condition of the nest tree (based on 25% increments of foliation), and predominant vegetation community at the nest site. Available nesting habitat was determined by measuring height and condition of all the trees along Birch Creek and those within 10 random 2-km stretches of the Big Lost River (hereafter referred to as available trees). Reference to nests refers to active hawk nests unless indicated otherwise.

We used Wilcoxon 2-way comparisons to determine interspecific differences in nest site characteristics ($\alpha \leq 0.05$). Food habits were compared using Shannon's (Shannon and Weaver 1949) and Pielou's (1969) diversity indices, as well as Pianka's (1973) overlap index. Estimates of prey biomass were obtained from Steenhof (1983).

RESULTS AND DISCUSSION

We noted considerably more red-tailed hawk nesting during our study than was reported for the INEL in 1974–76, when only one active nest was located (Craig 1979). Four active red-tailed hawk nests were noted on the entire INEL in 1982 and 1987 (Craig et al. 1984, J. Kirkley unpubl. data), and we found 8, 13, and 12 nests from 1991–93 on the entire INEL
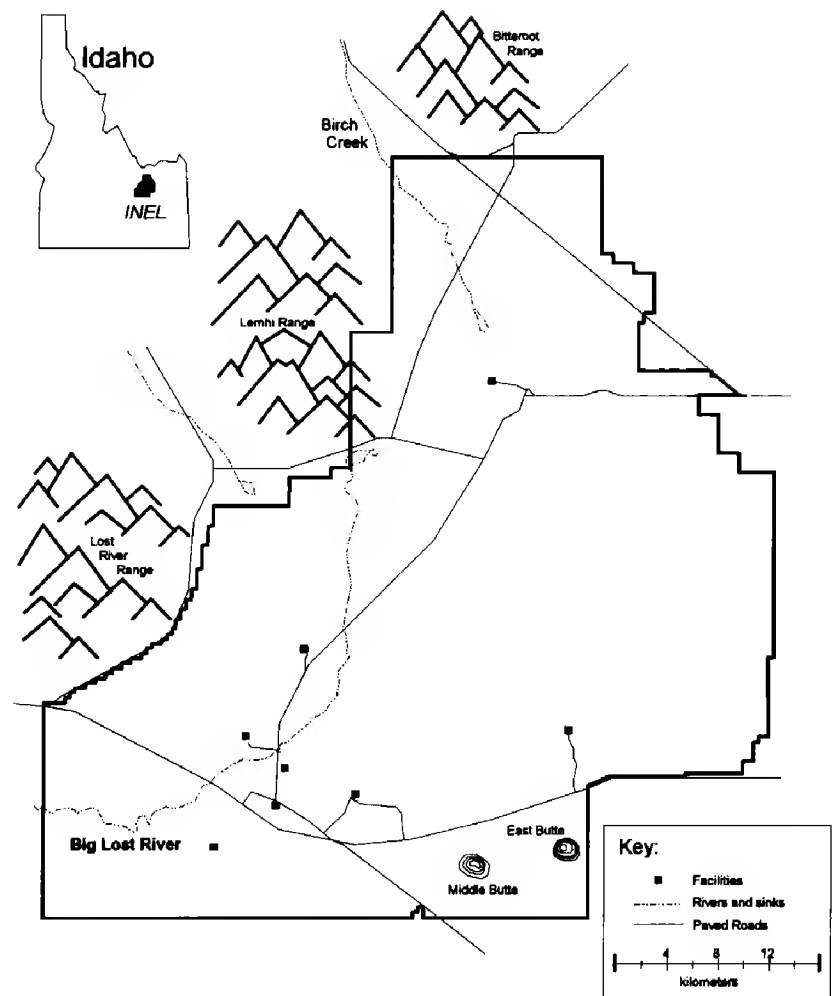

Figure 1. The Idaho National Engineering Laboratory showing relative locations of the Big Lost River, Birch Creek, and site facilities.

(Hansen 1994). All but nine of the red-tailed hawk nests we found were in deciduous trees along the Big Lost River; no nests were found on Birch Creek. Platt (1971) and Thurow et al. (1980) also found that red-tailed hawks in desert regions of northern Utah and southern Idaho selected deciduous trees for nesting.

The Swainson's hawk nesting populations on the INEL appear to have increased from the mid-1970s through our study. Craig (1979) found 12 active Swainson's hawk nests on the INEL over a 3-yr period from 1974–76, mostly along the Big Lost River. All nests located by Craig on the INEL in the 1970s were in deciduous trees along water courses or near agricultural areas. Seven active Swainson's hawk nests were located on the INEL in 1982 (Craig et al. 1984). We found 8, 10, and 10 active Swainson's hawk nests on the entire INEL for the years from 1991–93. Seventeen of 28 Swainson's hawk nests in our study were along the Big Lost River and Birch Creek, 16 of which were in deciduous trees; nine of the 17 nests were located on Birch

Table 1. Productivity of red-tailed and Swainson's hawks nesting along the Big Lost River and Birch Creek on the Idaho National Engineering Laboratory, 1991–93.

		NUMBER OF OCCUPIED NESTS	NUMBER OF NESTLINGS[a]	NUMBER OF FLEDGLINGS	NUMBER OF SUCCESSFUL NESTS[b]	FLEDGLINGS PER SUCCESSFUL NEST	FLEDGLINGS PER NEST
Red-tailed	1991	7	13	13	7	1.9	1.9
hawk	1992	9	22	15	7	2.1	1.7
	1993	8	19	6	3	2.0	0.8
Swainson's	1991	4	8	7	4	1.8	1.8
hawk	1992	6	13	8	5	1.6	1.3
	1993	7	14	6	4	1.5	0.9

[a] Minimum number.
[b] Nests that fledged at least one nestling.

Creek. The remainder of the Swainson's hawk nests were in junipers scattered around the INEL (Hansen 1994). Earlier nest surveys were conducted with methods similar to ours (Craig 1979, Craig et al. 1984); i.e., most of the INEL was searched and potential habitat and nest sites were investigated.

Red-tailed hawk productivity was similar to Swainson's hawk productivity on a per nest basis for the combined Big Lost River and Birch Creek areas during our study (Table 1). High nest failure occurred in red-tailed hawks in 1993, primarily due to structural failure of nests or nestling exposure to unusually cold, wet weather. Swainson's hawks along the Big Lost River and Birch Creek also had high failure rates, but the three nests found in junipers elsewhere on the INEL all fledged young (Hansen 1994). Red-tailed hawks tended to produce more fledglings per successful nest than Swainson's hawks in 1992 and 1993. Swainson's hawk productivity was highly variable by year in our study but fell within the range reported in the literature (Craighead and Craighead 1956, Platt 1971, Craig 1979, Fitzner et al. 1981, Gilmer and Stewart 1984). Red-tailed hawk production per nesting attempt on the Big Lost River (no nesting on Birch Creek) was similar to that noted in other studies (Johnson 1975, Wiley 1975, Fitzner et al. 1981). We could not compare clutch sizes because we waited until after incubation to begin nest visits in order to minimize nest desertion.

Red-tailed hawks nested in taller trees than Swainson's hawks ($Z = 3.28$, $P = 0.001$; Fig. 2); red-tailed hawk nest trees were also taller than trees occurring randomly along the Big Lost River ($Z =$ 2.76, $P = 0.006$). Correspondingly, red-tailed hawk nest trees had the larger dbh (median = 44 cm, quartiles = 42–52 cm) than Swainson's hawk nest trees (median = 29 cm, quartiles = 15–36 cm; $Z =$ 5.49, $P = 0.001$). The affinity of red-tailed hawks for tall nesting substrates has been reported by several investigators (Schmutz et al. 1980, Thurow et al. 1980, Bechard et al. 1990, Restani 1991). Both species tended to nest in trees that were taller than the average height of trees in the surrounding stands ($Z = 5.17$, $P = 0.001$; Fig. 2), but they did not necessarily nest in the tallest tree in that stand.

Swainson's hawk nests were smaller in diameter (median = 53 cm, quartiles = 43–59 cm) than red-tailed hawk nests (median = 57 cm, quartiles = 55–72 cm), but the difference was not significant ($Z =$ 1.19, $P = 0.23$). Both species occasionally used old ferruginous hawk (*Buteo regalis*) nests, but most nests along the Big Lost River and Birch Creek were constructed by the hawks nesting in them. Swainson's hawk nests rarely survived more than a year due to their flimsy nature, so they were not reused. The flimsy nature of Swainson's hawk nests was noted elsewhere (Call 1978).

Swainson's hawks nested in trees with more foliage (median = 75%, quartiles = 25–100%) than did red-tailed hawks (median = 0%, quartiles = 0–25%); they also nested in trees with more foliage than the trees occurring randomly along the Big Lost River and Birch Creek (median = 0%, quartiles = 0–25%; $Z = 2.27$, $P = 0.001$). Concealment or shading of nests may have been reasons for Swainson's hawk selection of well-foliated trees. Thermoregulation has been cited as a factor possibly affecting

the nest placement of other raptor species (Bednarz and Dinsmore 1982, Viñuela and Sunyer 1992). Other studies also found that Swainson's hawks' nests were similarly concealed in foliage (Dunkle 1977, Thurow and White 1983), but the relationship between nest site selection and tree condition (foliation) is not well-documented.

Degradation of deciduous trees along the Big Lost River and Birch Creek may be a factor influencing Swainson's hawk nesting in these areas. Swainson's hawks clearly displayed an affinity for well-foliated trees during our study, but such trees are becoming increasingly rare along the riparian corridors of the INEL. In the 1970s and early 1980s, the Big Lost River flowed on the INEL at least part of every year (Bennett 1990). Between 1987 and 1992 no water flowed on the study area due to a prolonged drought and diversion for irrigation west of the INEL. As a result, riparian vegetation along the channel degraded considerably. All the willow (*Salix* spp.) stands along the river were dead during our study. Cottonwood growth was curtailed, and by 1991 many mature trees were dead or dying; regeneration was almost nonexistent. Only three living cottonwoods <20 cm dbh were noted during our surveys of available nest trees along 20 km of the Big Lost River (Hansen 1994). Trees along Birch Creek were in better condition; 21 small trees were living along the 8 km we surveyed, but most of the trees along this channel were also seriously degraded. The only saplings we noted were associated with the roots of large trees (>45 cm dbh).

The degradation of Swainson's hawk nesting habitat along the Big Lost River may have benefitted red-tailed hawks by reducing direct interaction between the species and potentially increasing productivity. Interspecific interactions between red-tailed and Swainson's hawks can result in loss of some territory to the later nesting Swainson's hawk (Janes 1994). While territory loss to Swainson's hawks may not have a direct effect on red-tailed hawk nesting success (Janes 1984), factors affecting prey delivery may be deleterious to successful reproduction (Stinson 1980, Cress and Langley 1988).

No significant differences were found between red-tailed and Swainson's hawks in distances to human activity or in vegetation communities surrounding the nest site (sagebrush dominated grassland) on the Big Lost River. This may have been a result of the concentration of human activity along the Big Lost River (Fig. 1), and relatively monotypic vegetational
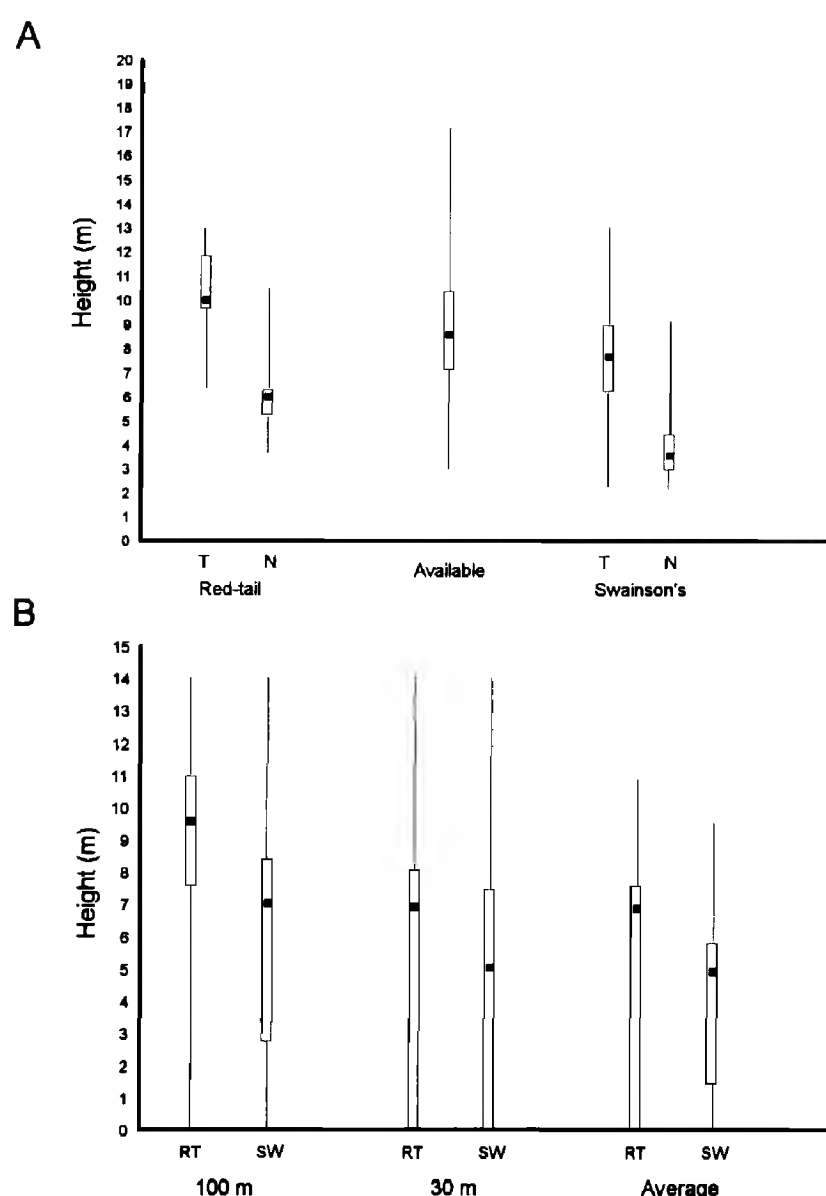

Figure 2. Box plots (median ± quartiles, range) of tree heights along the Big Lost River and Birch Creek on the Idaho National Engineering Laboratory: (A) nest (N) and nest tree (T) heights of red-tailed hawk and Swainson's hawk nest sites, and height of available trees; (B) tallest tree within 30 and 100 m of hawk nests and average height of trees within 30 m of nest tree.

communities along this corridor (McBride et al. 1978).

Continued degradation of vegetation along the Big Lost River and Birch Creek will probably result in decreased Swainson's hawk nesting along these channels. Tree condition appears to be a major factor influencing their nesting along these channels, and reduction of narrowleaf cottonwoods and western water birch (on Birch Creek) may reduce the suitability of this area for Swainson's hawk nesting. Without regular stream flow, the lack of deciduous tree regeneration and collapse of dead trees will eventually make these watercourses unsuitable for all tree-nesting raptors. As a result, a greater proportion of red-tailed and Swainson's hawks will have

Table 2.   Prey of nesting red-tailed (19 nests, 55 items) and Swainson's hawks (11 nests, 35 items) along the Big Lost River and Birch Creek on the Idaho National Engineering Laboratory, 1991–93, determined from prey remains and castings (expressed as percent frequency of occurrence and percent of total ingested biomass).

PREY CATEGORY	RED-TAILED HAWK		SWAINSON'S HAWK	
	% FREQ.	% BIOMASS	% FREQ.	% BIOMASS
Microtus spp.	21.9	2.3	11.4	2.3
Neotoma spp.	3.6	3.0	2.9	4.5
Other Cricetidae	10.9	0.4	22.9	1.7
Thomomys spp.	9.1	5.9	11.4	14.1
Sciuridae	9.1	2.8	2.9	1.7
Sylvilagus spp.	21.9	28.2	17.1	42.3
Lepus spp.	12.7	50.5	2.9	21.7
Aves	3.6	4.2	25.7	11.4
Reptilia	7.2	2.7	2.9	0.3
Diversity				
Shannon's Index[a]	0.99	0.62	1.07	0.72
Pielou's Index[b]	0.86	0.54	0.89	0.59

[a] Shannon and Weaver (1949).
[b] Pielou (1969).

to nest in junipers or move away from the INEL. During this study, 24 of 33 (73%) red-tailed hawk nests on the INEL were in cottonwoods along the Big Lost River and 16 of 28 (57%) Swainson's hawk nests on the INEL were in cottonwoods or birches along the river and Birch Creek (Hansen 1994).

Based on frequency of prey occurrence, both species had fairly broad diets (Table 2). Dietary overlap was high between these species using both frequency (0.83) and biomass (0.95) measures. Lagomorphs accounted for over 50% of the estimated biomass of prey items and accounted for much of the dietary overlap. However, red-tailed hawks tended to feed on *Lepus* and *Sylvilagus* spp. while Swainson's hawks took primarily *Sylvilagus* spp. Red-tailed hawks preyed more commonly on Sciuridae and reptiles than did Swainson's hawks. Swainson's hawks commonly preyed on birds as observed by Craig (1979) although, differing from our results, Craig did not find *Thomomys* spp. in the diets of Swainson's hawks. In contrast to our results, Schmutz et al. in Alberta recorded a higher frequency and biomass of birds in the diet of red-tailed hawks than in Swainson's hawks. Invertebrates were common in Swainson's hawk pellets, but we were unable to quantify their occurrence.

Birds and invertebrates were underrepresented using our method of food habits analysis, potentially inflating our measure of dietary overlap (Simmons et al. 1991). Additionally, our sample sizes were small, so caution should be exercised when interpreting these data. However, some generalizations can be made. Lagomorphs were an important prey item for both species. Lagomorphs, especially black-tailed jackrabbits (*Lepus californicus*), are an important prey resource for *Buteo*s throughout this region (Platt 1971, Craig 1979, Thurow et al. 1980, Smith et al. 1981). Black-tailed jackrabbit populations fluctuate greatly on the study area (French et al. 1965, Johnson and Anderson 1984). Black-tailed jackrabbit densities were low during our study and during the mid-1970s (Craig 1979). Craig et al. (1984) reported an increase in nesting Swainson's and red-tailed hawks during 1982, a year of high densities of black-tailed jackrabbits. However, numbers of nesting Swainson's hawks and red-tailed hawks in our study, a period of low black-tailed jackrabbit numbers, were even higher than in 1982 (Craig et al. 1984). Additional monitoring of this raptor community during a period of black-tailed jackrabbit abundance would provide insight into the effects of this prey on the ecological relationships between nesting Swainson's and red-tailed hawks.

We suspect that nesting red-tailed and Swainson's hawks were primarily concentrated near riparian areas because of the location of nesting trees. However, habitat along the Big Lost River, Birch Creek, and riparian areas in general, may also provide an increased diversity of prey species for nesting hawks. Unfortunately, our sample sizes are not adequate for comparing diets of upland nesting raptors versus those nesting on Big Lost River or Birch Creek. The situation along the Big Lost River underscores the fact that indirect human disturbance can affect the viability of raptor assemblages as much as direct habitat destruction. Provisions for allowing minimal but periodic flow of water to ensure adequate regeneration of narrowleaf cottonwood along the Big Lost River and Birch Creek would be particularly valuable to red-tailed and Swainson's hawks.

LITERATURE CITED

BECHARD, M.J., R.L. KNIGHT, D.G. SMITH AND R.E. FITZNER. 1990. Nest sites and habitats of sympatric hawks (*Buteo* spp.) in Washington. *J. Field Ornithol.* 61:159–170.

BEDNARZ, J.C. AND J.J. DINSMORE. 1982. Nest sites and habitat of red-shouldered and red-tailed hawks in Iowa. *Wilson Bull.* 94:31–45.

BENNETT, C.M. 1990. Streamflow losses and groundwater level changes along the Big Lost River at the Idaho National Engineering Laboratory, Idaho. USGS Water-Res. Invest. Rep. 90-4067. Idaho Falls, ID U.S.A.

CALL, M.W. 1978. Nesting habitats and surveying techniques for common western raptors. USDI, Bur. Land Manage. Tech. Note TN-316, Denver, CO U.S.A.

CLAWSON, K.L., G.E. START AND N.R. RICKS. 1989. Climatography of the Idaho National Engineering Laboratory. DOE/ID-12118. USDC, NOAA, Environ. Res. Lab., Air Resources Lab. Field Res. Div., Idaho Falls, ID U.S.A.

CRAIG, T.H. 1979. The raptors of the Idaho National Engineering Laboratory site. IDO-12089. USDE, Idaho Falls, ID U.S.A.

———, E.H. CRAIG AND L.R. POWERS. 1984. Recent changes in buteo abundance in southeastern Idaho. *Murrelet* 65:91–93.

CRAIGHEAD, J.J. AND F.C. CRAIGHEAD. 1956. Hawks, owls, and wildlife. Stackpole, Harrisburg, PA U.S.A.

CRESS, G.A. AND W.M. LANGLEY. 1988. Effect of annual and habitat variations in prey on the growth and productivity of red-tailed hawks (*Buteo jamaicensis*). *Trans. Kans. Acad. Sci.* 91:96–102.

DUNKLE, S.W. 1977. Swainson's hawks on the Laramie Plains, Wyoming. *Auk* 94:65–71.

FITZNER, R.E., W.H. RICKARD, L.L. CADWELL AND L.E. RODGERS. 1981. Raptors of the Hanford Site and nearby areas of southcentral Washington. PNL-3212, Pacific Northwest Laboratory, Richland, WA U.S.A.

FRENCH, N.R., R. MCBRIDE AND J. DETMER. 1965. Fertility and population density of the black-tailed jackrabbit. *J. Wildl. Manage.* 29:14–26.

GILMER, D.S. AND R.E. STEWART. 1984. Swainson's hawk nesting ecology in North Dakota. *Condor* 86:12–18.

HANSEN, R.W. 1994. Raptor use of the Idaho National Engineering Laboratory. M.S. thesis, South Dakota State Univ., Brookings, SD U.S.A.

JANES, S.W. 1984. Influences of territory composition and interspecific competition on red-tailed hawk reproductive success. *Ecology* 65:862–870.

———. 1994. Partial loss of red-tailed hawk territories to Swainson's hawks: relations to habitat. *Condor* 96:52–57.

JOHNSON, R.D. AND J.E. ANDERSON. 1984. Diets of black-tailed jackrabbits in relation to population density and vegetation. *J. Range Manage.* 37:79–83.

JOHNSON, S.J. 1975. Productivity of the red-tailed hawk in southwestern Montana. *Auk* 92:732–736.

MARTI, C.D. 1987. Raptor food habits studies. Pages 67–80 *in* B.A. Giron Pendleton, B.A. Millsap, K.W. Cline and D.M. Bird [EDS.], Raptor management techniques manual, Natl. Wildl. Fed., Washington, DC U.S.A.

MCBRIDE, R., N.R. FRENCH, A.H. DAHL AND J.E. DETMER. 1978. Vegetation types and surface soils of the Idaho National Engineering site. IDO-12084 Idaho Operations Office, USDE, Idaho Falls, ID U.S.A.

NEWTON, I. 1976. Population limitation in diurnal raptors. *Can. Field-Nat.* 90:274–300.

PIANKA, E.R. 1973. The structure of lizard communities *Annu. Rev. Ecol. Syst.* 4:53–74.

PIELOU, E.C. 1969. An introduction to mathematical ecology. Wiley Interscience, New York, NY U.S.A.

PLATT, J.B. 1971. A survey of nesting hawks, eagles, falcons, and owls in Curlew Valley, Utah. *Great Basin Nat.* 31:51–65.

RESTANI, M. 1991. Resource partitioning among three *Buteo* species in the Centennial Valley, Montana. *Condor* 93:1007–1010.

SCHMUTZ, J.K. 1984. Ferruginous and Swainson's hawk abundance and distribution in relation to land use in southeastern Alberta. *J. Wildl. Manage.* 48:1180–1187.

———, S.M. SCHMUTZ AND D.A. BOAG. 1980. Coexistence of three species of hawks (*Buteo* spp.) in the prairie-parkland ecotone. *Can. J. Zool.* 58:1075–1089

SHANNON, C.E. AND W. WEAVER. 1949. The mathematical theory of communication. Univ. Ill. Press, Urbana, IL U.S.A.

SIMMONS, R.E., D.M. AVERY AND G. AVERY. 1991. Biases in diets determined from pellets and remains: correction factors for a mammal and bird-eating raptor *J. Raptor Res.* 25:63–67.

SMITH, D.G., J.R. MURPHY AND N.D. WOFFINDEN. 1981. Relationships between jackrabbit abundance and ferruginous hawk reproduction. *Condor* 83:52–56.

STEENHOF, K. 1983. Prey weights for computing percent biomass in raptor diets. *Raptor Res.* 17:15–27.

STINSON, C.H. 1980. Weather-dependent foraging success and sibling aggression in red-tailed hawks in central Washington. *Condor* 82:76–80.

THUROW, T.L. AND C.M. WHITE. 1983. Nest site relationship between the ferruginous hawk and Swainson's hawk. *J. Field. Ornithol.* 54:401–406.

———, C.M. WHITE, R.P. HOWARD AND J.F. SULLIVAN. 1980. Raptor ecology of Raft River Valley, Idaho EGG-2054. EG&G Idaho, Idaho Falls, ID U.S.A.

VIÑUELA, J. AND C. SUNYER. 1992. Nest orientation and hatching success of black kites *Milvus migrans* in Spain. *Ibis* 134:340–345.

WILEY, J.W. 1975. The nesting and reproductive success of red-tailed hawks and red-shouldered hawks in Orange County, California. *Condor* 77:133–139.

SCALING SWAINSON'S HAWK POPULATION DENSITY FOR ASSESSING HABITAT USE ACROSS AN AGRICULTURAL LANDSCAPE

K. Shawn Smallwood
EIP Associates, 1200 Second Street, Suite 200, Sacramento, CA 95814 U.S.A.

Abstract.—By integrating population density estimates of Swainson's hawk (*Buteo swainsoni*) from other studies, I found that the areas within study boundaries consistently support much higher densities of Swainson's hawk than do the surrounding areas, and most of the variation in density was explained by the spatial extent of study. Therefore, I designed a sampling program to express habitat use across multiple potential clusters of home ranges, thereby representing the population-level interaction with the agricultural landscape of the Sacramento Valley, CA. I mapped 162 observations of Swainson's hawks in 5 yr of surveys (110 surveys) along a 204-km road transect from a car traveling at 80–88 kph. Based on use and availability of landscape elements along the transect, Swainson's hawks "preferred" riparian habitat, grassland, alfalfa stands >2 yr old during irrigation and mowing, and annual field crops during harvest. Hawks "avoided" most other crops, tilled fields, and built-up areas.

Key Words: *Agriculture*; *alfalfa*; Buteo swainsoni; *density*; *road survey*; *Sacramento Valley*; *Swainson's hawk.*

Escalamiento de la densidad poblacional de *Buteo swainsoni* para evaluar uso de hábitat a través de un paisaje agrícola

Resumen.—Por integración de densidades poblacionales de *Buteo swainsoni* estimadas en otros estudios, encontré que áreas de borde, en estudio, consistentemente soportaban mayores densidades de esta especie que las áreas vecinas y la mayoría de la variación en densidad era explicada por la extensión espacial del estudio. De manera que diseñe un programa de muestreo para expresar uso de hábitat a través de racimos potenciales multiples de rangos de hogar, representando asi, la interacción a nivel poblacional con el paisaje agrícola de Valle de Sacramento, California. Se mapearon 162 observaciones de *B. swainsoni* en cinco años de recorridos (110 recorridos) a lo largo de un transecto carretero de 204 km, realizado en un vehículo viajando a 80–88 kph. Basados en el uso y disponibilidad de elementos del paisaje a lo largo del transecto, *B. swainsoni* "prefirió" hábitat ribereños, praderas y campos de alfalfa mayores a dos años de antiguedad durante la irrigación, corte y durante la cosecha anual de los campos. *Buteo swainsoni* "evitó" otros tipos de cosechas, campos cultivados y áreas de construcción.

[Traducción de Ivan Lazo]

Knowledge of the ecological resources needed by the Swainson's hawk (*Buteo swainsoni*) is important because the species is thought to have declined radically in California (Bloom 1980), and is now listed as threatened there. This knowledge is also important because Swainson's hawk management decisions, including mitigation for development, and state and federal recovery plans, affect large investments in agriculture and construction. Swainson's hawk populations are threatened by land conversions and management decisions that leave enough ecological resources for only a minimum existence (Wilcox 1989).

Most Swainson's hawk habitat-use studies occurred within small areas immediately around nest trees or within home ranges (e.g., Gilmer and Stew-art 1984, Estep 1989, Bechard et al. 1990). These intensive studies were typically constrained to small geographic areas because they were expensive and thus were required to be focused on a small number of individuals. The results of these local studies sometimes have been extrapolated to estimate habitat use in larger regions (e.g., Bloom 1980, Bednarz and Hoffman 1988), which then could be used for management decisions, without making adjustments for changes in landscape attributes nor for changes in Swainson's hawk spatial pattern.

The regional context is usually excluded from analyses during population and habitat-use studies. Such intensive studies of most species usually occur where the investigator(s) had *a priori* knowledge of high density (Schonewald and Smallwood in press).

The home range is often viewed as the spatial requirement of a species, so habitat associations are derived from observations within the home ranges. But nesting pairs choose locations for their home ranges from among many potential locations within their historic geographic range. Studies at high-density sites might not provide all the information that is needed for management of the Swainson's hawk at a regional scale. Density estimates and habitat use at small study sites could be reliably extrapolated to the region only if Swainson's hawks and habitats (and land use) are uniformly distributed across the landscape. Distribution maps of nesting pairs suggest that Swainson's hawks in California are highly aggregated (Bloom 1980, Schlorff and Bloom 1984, Estep 1989). The clusters of nest sites are where most investigations have been conducted (Schmutz et al. 1980, Gilmer and Stewart 1984, and Estep 1989).

In this paper I first test whether Swainson's hawks are uniformly distributed across studied landscapes, which would be a necessary condition for extending the results of population and habitat-use studies to larger areas. Then I complement results of intensive studies with those of a survey along an extensive road transect in the Sacramento Valley, California. The road transect was designed to sample a geographic area that was much larger than conventional population and habitat-use study areas of the valley's largest birds and mammals, and the types of agriculture that occur in the valley (Smallwood et al. in press). By exceeding the areas of conventional habitat-use studies, I was able to critically analyze the effects of agricultural crops and practices on a Swainson's hawk population.

METHODS

Scaling Population Density. From 26 population estimates in 16 research reports of Swainson's hawk studies, I recorded every estimate of nesting density within each geographic area defined for study. I used the geometric mean for multi-annual estimates made at a site. Schmutz (1984) was not used because he sampled only 4.4% of his 74 686 km^2 study area. Log$_{10}$ transformed estimates of nesting density (pairs per square kilometer) were tested for linear relationships with the spatial extent of studies with the equation:

$$\text{Log}_{10}(\text{nesting density}) = a - b \times \text{log}_{10}(\text{area}), \quad (1)$$

where a and b are the intercept and slope coefficients to be estimated with least squares regression. Model precision was assessed by examining the coefficient of determination (R^2), the root mean square error of the residuals (RMSE), and the pattern of residuals plotted against study

area. The spatial pattern of Swainson's hawks across studied landscapes is increasingly homogenous (aggregated to random to uniform) as the regression slope approaches 0 in equation (1). If the hawks' spatial pattern is found to be far from homogenous, then density estimates and habitat associations cannot be reliably extrapolated to areas that are larger than the conventional study areas.

Habitat Associations. My road transect was designed to sample wildlife populations across a large geographic area in which interactions between species and the landscape could be measured. It was designed to sample interspersed landscape elements in the Sacramento Valley, including the major types of agriculture produced (field crops, rice, orchards, and pasture), along with urban and rural areas, riparian habitat, and grassland and wetland habitats in protected areas. It was also designed to provide extensive north-to-south and east-to-west coverage. The road transect was 204 km in seven segments (to provide rest periods for the investigator) along a 320-km loop around the Sutter Buttes (described further in Smallwood et al. in press).

I surveyed for wildlife from the passenger seat of a car driven at 80–88 kph at 1 wk to 1 mo intervals. Surveys always began 0700–0930 H, and typically lasted 5 hr. For multiple bird and mammal species, I recorded the species, activity, land-use/habitat association, location to the nearest 0.16 km, and side of road where the observation occurred. I mapped the crops immediately along the transect, including tilled fields, crop residues, and agricultural activities such as harvest, irrigation, and tillage. Swainson's hawk observations from 3306 km of survey (57 surveys) along the first 58 km of the transect (Davis to Sutter National Wildlife Refuge) were related to land-use and habitat elements based on the proportional occurrence of each (after Smallwood 1993, Smallwood et al. in press)

Swainson's hawk's use of alfalfa fields was further investigated during a 2-yr (1992–94) study of pocket gopher (*Thomomys bottae*) spatial dynamics in 36 Sacramento Valley alfalfa fields (Smallwood and Geng 1993b). While mapping gopher burrows by walking along borders of irrigated fields, I recorded Swainson's hawk visits from 0630–1200 H, March to September. I compared the number of visiting Swainson's hawks with my time spent in alfalfa fields of various ages and harvest phases; i.e., mowing, raking, baling hay, collecting bales.

RESULTS

Scaling Population Density. Nesting Swainson's hawks were aggregated across studied landscapes. The regression slope was significantly different from 0 ($P < 0.0001$) and substantially different from corresponding with homogeneity (Fig. 1A). The nesting density at the smallest study area was 124 times greater than the density at the largest study area when calculated from the regression, and the real difference was 310-fold. Also, the average number of pairs per 1 km^2 was calculated from the regression to be 2.2, which is more than can be expected at any randomly selected site across the Swainson's hawk

nesting range. Therefore, the Swainson's hawk studies used in the regression analysis were consistently conducted at sites where Swainson's hawk population densities were much higher than across the surrounding, unstudied areas.

All of the density estimates were made after intensive ground searches for nests, although Platt (1971) included aerial searches and Littlefield et al. (1984) searched from the road. The searches were reported to be complete or inclusive of all nests in 56% of the studies and 70% of the density estimates. However, whether or not the search was reported to be complete did not influence the residual variation that remained after density was regressed against study area (Independent samples $T = 0.59$, df $= 19$, $P = 0.56$). Instead, this residual variation appeared to cycle with a periodicity of about 10 yr (Fig. 1B). This possible, range-wide population cycle could not have been recognized from the existing data without removing the variation in density due to the spatial extent of study area.

Habitat Associations. I made 162 Swainson's hawk observations during the entire road survey, but only 130 were used in the habitat-use analysis from the cumulative 3306 km along the first 58 km of transect during March to October. My observations were nearly evenly distributed among months from March ($N = 24$) until October ($N = 13$). Most (82%) were of birds in flight, 11 (7%) were on trees, five (3%) were on the ground, and 7% were on artificial structures such as utility poles and fence posts. Swainson's hawks occurred more often than expected by chance in alfalfa, riparian, and grassland habitats, where they occurred throughout the breeding season (Fig. 2A). The remainder of the landscape elements were used by Swainson's hawks preferentially only during brief periods of opportunity; e.g., in tomato fields 21.7 times more often during harvest than expected by chance. The 16 Swainson's hawks I saw at tilled fields were during early spring and fall when most of the landscape was tilled or being tilled (Fig. 2B). Rice stubble left through the winter was used by Swainson's hawks during early spring, but overall rice stubble was avoided by Swainson's hawks. Safflower and some other crops were never used, not even after harvest (Fig. 2A).

Both the road survey and gopher sampling revealed that Swainson's hawks used alfalfa most often while those fields were being irrigated, and secondly during hay harvesting (Figs. 3 and 4). These preferences were greatest in alfalfa that was 3–4 yr old
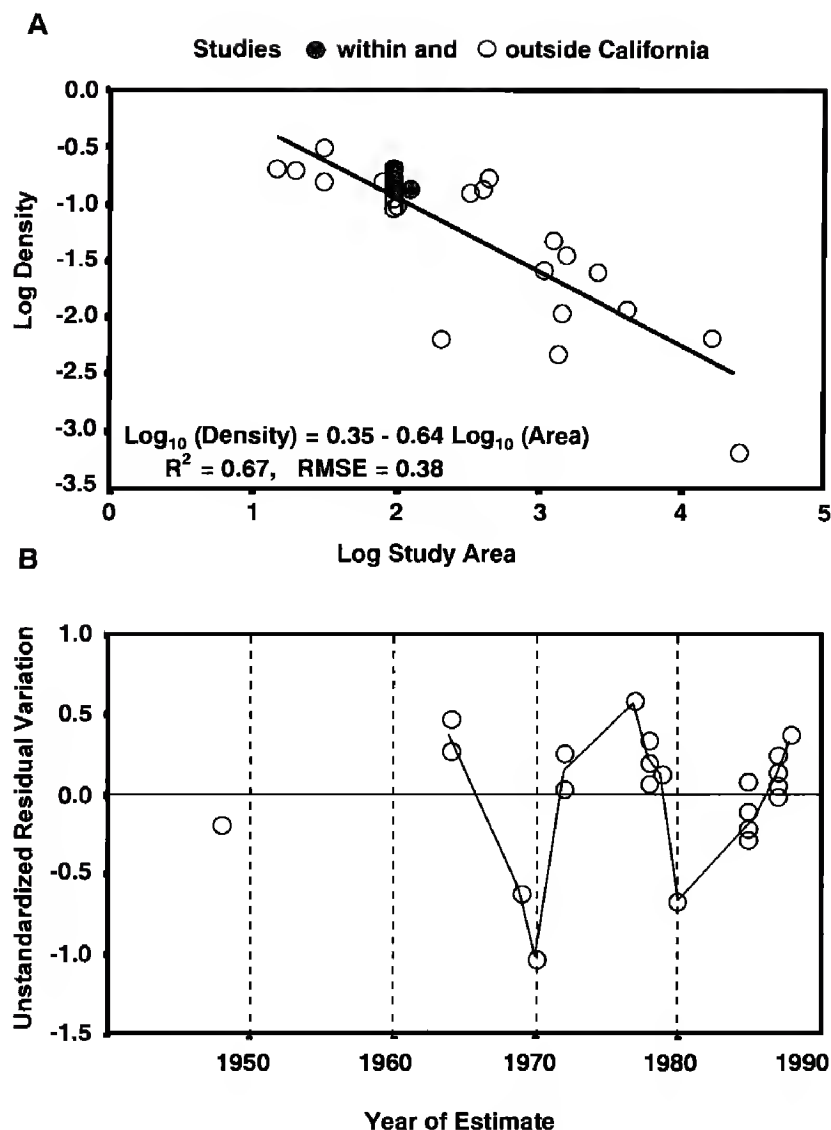

Figure 1.   Log-transformed estimates of Swainson's hawk population density decrease linearly with increasing log spatial extent of study area (A), and the residuals suggest an approximately 10-yr population cycle (B) fit by lowess smoothing on 20% of the data. Estimates were from Craighead and Craighead (1956), Platt (1971), Smith and Murphy (1973), Olendorff (1975), Dunkle (1977), Fitzner (1978), Bloom (1980), Schmutz et al. (1980), Bechard (1983), Littlefield et al. (1984), Bednarz and Hoffman (1988), Gilmer and Stewart (1984), Estep (1989), Restani (1991), and Bosakowski and Ramsey (unpubl. data).

(Figs. 3 and 4B). All of the 31 Swainson's hawks seen in alfalfa fields during the road survey were at fields being irrigated, which comprised 0.02% of the transect. Thus, Swainson's hawks were 858 times more likely to occur at mowed and irrigated alfalfa fields than if they occurred randomly along the transect.

DISCUSSION

Scaling Population Density. Most of the variation in Swainson's hawk density was explained by

A

Number of Observations

During | growth period | harvest season

Observed Expected Number

Habitat	Data (Month 3–10)	Observed / Expected
Rice	4 2 ... 2 1	0.0 0.6
Corn		0.0
Safflower		0.0
Sunflower		0.0
Sorghum		0.0
Wheat	1 5 1 1 .1 .1	0.1
Beans		0.0
Melons		0.0
Squash	1	0.1
Tomatoes	1 ... 1 1 4 2 2 ... 2	0.9 4.7
Sugarbeets		0.0
Alfalfa	1 2 ... 4 23 1 ... 1	8.2 858
Barley Hay	1	1.6
Tilled	1 2 2 ... 2 ... 4 1 4	0.6
Orchards	4	0.7
Built-up	1	0.1
Riparian, Grassland	3 7 4 1 4 2 2 1 3 10 1 1 1	4.7 3.7

Month   3   4   5   6   7   8   9   10

B

Percent of Transect — 0, 10, 20, 30, 40, 50, 60, 70

Legend:
— Annual Crop residue
— Grain stubble
..... Rice stubble

Labels: Tilled, Grains, Annual field crops, Rice

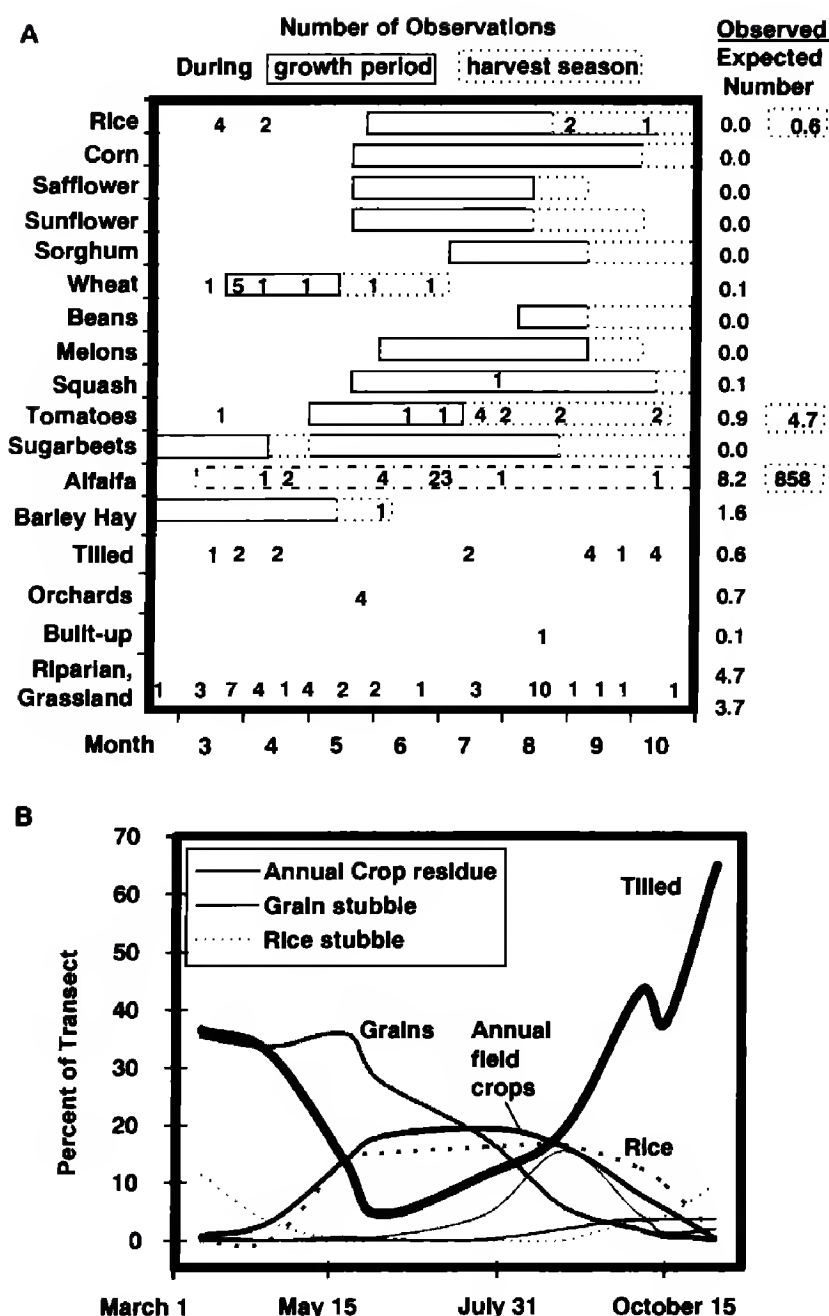X-axis: March 1   May 15   July 31   October 15

Figure 2. The Swainson's hawk distribution among habitats during the nesting seasons of 1990–94 (A) and the 1993–94 moving average of agricultural field conditions expressed as a percent of the southern 58 km of the road transect (B). Expected values are the total number of hawks observed multiplied by the proportion of each habitat in the sample.

the spatial extent of study, consistent with results for other species (Schonewald and Smallwood in press). This means that most study methods have little influence on density estimates, if the methods are rigorous. Except for Schmutz (1984), the residual variation in density estimates based on different methods plotted precisely along the lowess curve that suggests a population cycle (Fig. 1B). Clearly, results from conventional studies cannot be extrapolated to larger geographic areas without at least making analytical adjustments for the change in spatial scale.

Judging from the scientific literature, investigators were previously unaware of the magnitude to which density changes with the spatial extent of study. Bloom (1980) multiplied his density estimate in the Klamath Basin by 0.25 (25% of the then known maximum density in California) to estimate the population size across the Swainson's hawk's historical range in California, which was estimated from topographic maps, field surveys, and the literature. Bloom's minimum estimate was 4284 pairs and his maximum estimate was 17 136 pairs. Using the model in Fig. 1, I calculated a mean population 404 pairs (SD = 166) across this historic range, which falls between the estimates of 375 and 550 pairs for 1979 (Bloom 1980) and in 1988 (California Department of Fish and Game 1990), respectively, and which is much less than Bloom's historic estimates. But my calculation should not be expected to be a reliable estimate of the historic Swainson's hawk population. The regression model in Fig. 1 can provide precise estimates within the data range (high to low values of densities and study areas), but is less reliable for an estimate across the historic distribution, because we do not know whether the log-log relationship between density and area remains infinitely linear. The habitat conditions have been altered radically, so there could have been more Swainson's hawks based on habitat availability. Nevertheless, the population might not have been much larger because it was naturally aggregated despite habitat availability, and the regression model showed that study areas such as Bloom's (1980) typically have much higher densities than areas not studied.

Study areas may be fundamentally different from the surrounding areas. The average square kilometer of land does not support 2.2 pairs of Swainson's hawks as predicted by the regression model in Fig. 1. Study areas are probably dissimilar to unstudied areas in terms of habitat conditions, but habitat-use studies only occur within the boundaries of study areas. Little connection has been made between habitat conditions on study areas and those beyond the study boundaries. Therefore, different habitats on study areas are used significantly more and less than if the study boundary encompassed a much larger geographic area. My road survey was designed to complement conventional habitat-use studies by linking habitats in areas of Swainson's hawk aggregations with habitats in the surrounding landscape. Other road surveys have been conducted for Swain-

son's hawk habitat use, but the transects were arranged for a more intensive survey within the area of aggregations.

Habitat Associations. My survey design resulted in conclusions about habitat use by Swainson's hawks which differed from other reported studies. Swainson's hawk use of riparian habitat, grassland, and alfalfa were greater in my study, probably because the greater spatial extent of study provided a much lower estimate of the availability of these habitat types. In my study Swainson's hawks seemed to avoid irrigated pasture, tilled fields, annual field crops, and developed areas, probably because the availability of these habitat types was much greater across the larger landscape.

My results also show that the majority of the agricultural landscape is inhospitable to nesting Swainson's hawks most of the time (Fig. 3). Prey availability is usually greater during crop harvest when prey are exposed by the removal of the canopy that persisted during the growth period. Swainson's hawks opportunistically forage over field crops during or just following harvest or irrigation. But these opportunities occur briefly at each field. The brief foraging opportunities in alfalfa occur mostly in fields at least 2.5 yr old, after prey populations have increased to sufficient levels (Smallwood and Geng 1993a,b).

Conservation Implications. The most effective opportunities for Swainson's hawk conservation might be in the management of agricultural landscapes where nesting and foraging habitat limit population size. Swainson's hawk nesting density increased in cultivated areas where tree density (Schmutz 1984) and prey availability (Bechard 1982) were highest. Swainson's hawk conservation would benefit substantially from the protection and restoration of riparian forests with large cottonwoods and oaks, and by managing field borders, road verges, and canal banks as strip corridors of grasses and shrubs. The lack of movement corridors for small mammals in the Sacramento Valley probably decreased populations of small mammals (Smallwood 1994) which are prey of Swainson's hawks. Pocket gophers, one of the important prey species (Bechard 1982, 1983, Gilmer and Stewart 1984, Restani 1991), are controlled in many alfalfa fields because they are thought to reduce alfalfa yields. Vertebrate pest management could be altered to the benefit of Swainson's hawk by better understanding the relationship
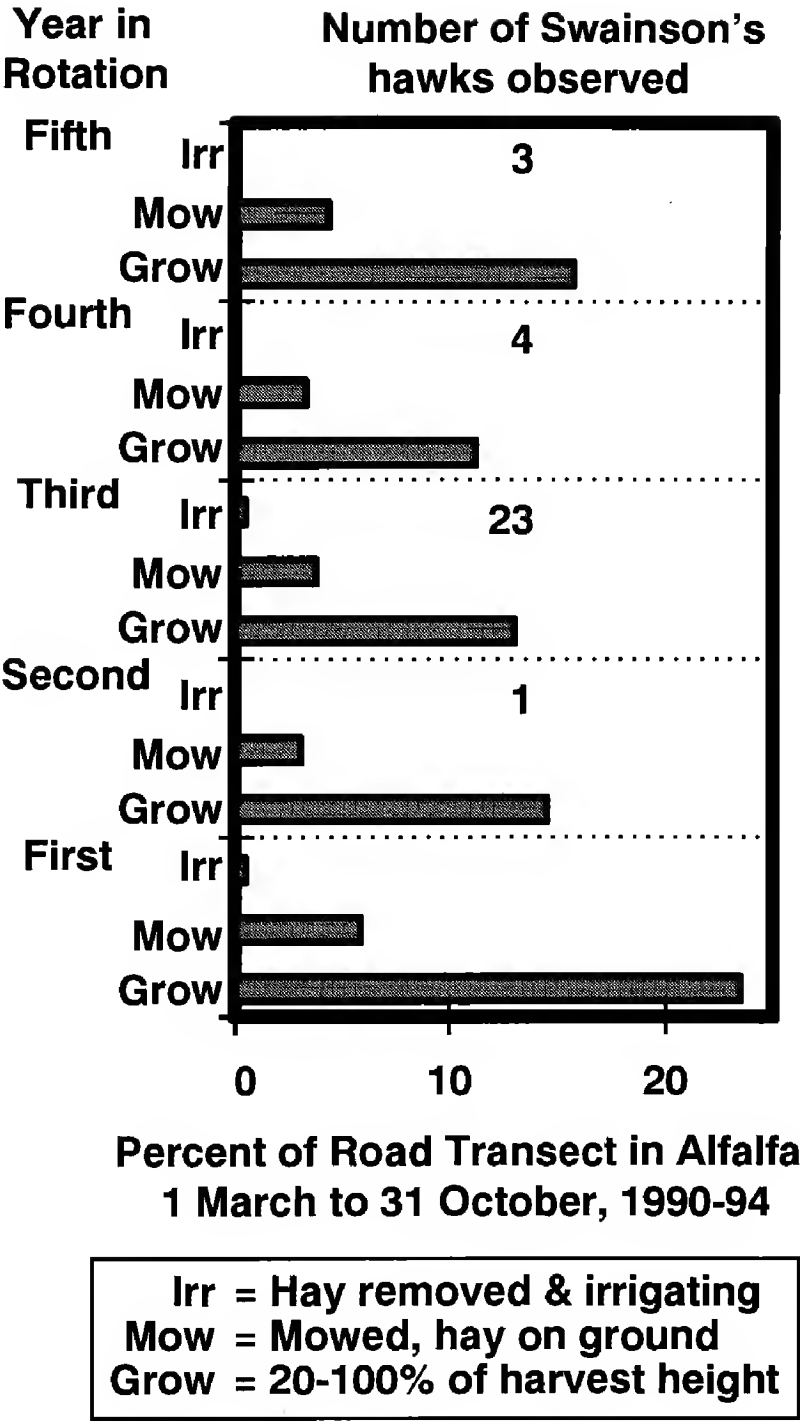

Figure 3. Swainson's hawk occurrences at alfalfa fields along the road transect.

between "pests" and agricultural crops. Van Vuren and Smallwood (in press) described many alternative vertebrate pest management strategies, most of which are not currently used. Even orchards and vineyards, which are generally considered to be poor Swainson's hawk foraging areas, can provide habitat for prey when cover crops are grown. Cover crops serve as habitat and alternative food (rather than the commercial crop) for small mammals, which will disperse into habitats that are more accessible to foraging Swainson's hawks. Thus, agriculture might actually benefit Swainson's hawks so long as the critical resources are maintained and/or enhanced.

LITERATURE CITED

BECHARD, M.J. 1982. Effect of vegetative cover on foraging site selection by Swainson's hawk. Condor 84: 153–159.

———. 1983. Food supply and the occurrence of brood reduction in Swainson's hawk. Wilson Bull. 95:233–242.

———, R.L. KNIGHT, D.G. SMITH AND R.E. FITZNER. 1990. Nest sites and habitats of sympatric hawks (Buteo spp.) in Washington. J. Field Ornithol. 61:159–170.

BEDNARZ, J.C. AND S.W. HOFFMAN. 1988. The status of breeding Swainson's hawks in southeastern New Mexico. Pages 253–259 in R.L. Glinski, B.G. Pendleton, M.B. Moss, M.N. Lefranc, Jr., B.A. Millsap and S.W. Hoffman [EDS.], Proceedings of the southwest raptor management symposium and workshop. Natl. Wildl. Fed. Sci. Tech. Ser. No. 11, Washington, DC U.S.A.

BLOOM, P.H. 1980. The status of the Swainson's hawk in California, 1979. Final Report II-8.0, Bureau of Land Management and Federal Aid in Wildlife Restoration, Projects W-54-R-12, The Resources Agency, California Dept. Fish and Game, Sacramento, CA U.S.A.

CALIFORNIA DEPARTMENT OF FISH AND GAME. 1990. Five year status report: Swainson's hawk. Nongame Bird and Mammal Sec., California Dept. Fish and Game, Sacramento, CA U.S.A.

CRAIGHEAD, J.C. AND F.C. CRAIGHEAD, JR. 1956. Hawks, owls and wildlife. The Stackpole Co., Harrisburg, PA U.S.A.

DUNKLE, S.W. 1977. Swainson's hawks on the Laramie Plains, Wyoming. Auk 94:65–71.

ESTEP, J.A. 1989. Biology, movements, and habitat relationships of the Swainson's hawk in the Central Valley of California, 1986–1987. California Dept. Fish and Game, Nongame Bird and Mammal Sec. Rep., Sacramento, CA U.S.A.

FITZNER, R.E. 1978. Behavioral ecology of the Swainson's Hawk (Buteo swainsoni) in Washington. Ph.D. dissertation. Washington State Univ., Pullman, WA U.S.A.

GILMER, D.S. AND R.E. STEWART. 1984. Swainson's hawk nesting ecology in North Dakota. Condor 86: 12–18.

LITTLEFIELD, C.D., S.P. THOMPSON AND B.D. EHLERS. 1984. History and present status of Swainson's hawks in southeast Oregon. Raptor Res. 18:1–5.

OLENDORFF, R.R. 1975. Population status of large raptors in northeastern Colorado—1970–1972. Pages 185–205 in J.R. Murphy, C.M. White and B.E. Harrell [EDS.], Population status of raptors. Raptor Res. Found. Inc., Vermillion, SD U.S.A.

PLATT, J.B. 1971. A survey of nesting hawks, eagles, falcons and owls in Curlew Valley, Utah. Great Basin Nat. 31:51–65.

RESTANI, M. 1991. Resource partitioning among three Buteo species in the Centennial Valley, Montana. Condor 93:1007–1010.

SCHLORFF, R.W. AND P.H. BLOOM. 1984. Importance of riparian systems to nesting Swainson's hawks in the Central Valley of California. Pages 612–618 in R.E. Warner and K.M. Hendrix [EDS.], California riparian systems—ecology, conservation, and productive management. Univ. California Press, Berkeley, CA U.S.A.

SCHMUTZ, J.K. 1984. Ferruginous and Swainson's hawk abundance and distribution in relation to land use in southeastern Alberta. J. Wildl. Manage. 48:1180–1187.

———, S.M. SCHMUTZ AND D.A. BOAG. 1980. Coexistence of three species of hawks (Buteo spp.) in the prairie-parkland ecotone. Can. J. Zool. 58:1075–1089.

SCHONEWALD, C. AND K.S. SMALLWOOD. A century's trends in the study of mammalian carnivore populations. In P. Opler [ED.], Status and trends. USDI Natl. Biol. Serv., Washington, DC U.S.A. In press.

SMALLWOOD, K.S. 1993. Understanding ecological pattern and process by association and order. Acta Oecol. 14:443–462.

———. 1994. Site invasibility by exotic birds and mammals. Biol. Conserv. 69:251–259.

——— AND S. GENG. 1993a. Alfalfa as wildlife habitat. Calif. Alfalfa Symp. 23:105–108.

——— AND ———. 1993b. Management of pocket gophers in Sacramento Valley alfalfa. Calif. Alfalfa Symp 23:86–89.

———, B.J. NAKAMOTO AND S. GENG. Association analysis of raptors and turkey vulture in an agricultural landscape. In D.M. Bird, D.E. Varland and J.J. Negro [EDS.], Raptor adaptations to human influenced environments. Academic Press, London, U.K. In press

SMITH, D.G. AND J.R. MURPHY. 1973. Breeding ecology of raptors in the eastern Great Basin of Utah. Brigham Young Univ. Sci. Bull. Biol. Ser. 18:1–71.

VAN VUREN, D. AND K.S. SMALLWOOD. 1995. Ecological

management of vertebrate pests in agricultural systems. *Biol. Agric. & Hortic.* In press.

Wilcox, B.A. 1989. The long-term consequences of environmental perturbations on raptor populations. Pages 263–270 *in* B.C. Pendleton, C.E. Ruibal and D.L. Krahe [Eds.], Western raptor management symposium and workshop. Natl. Wildl. Fed. Sci. Tech. Ser. No. 12, Washington, DC U.S.A.

NEST-SITE SELECTION AND REPRODUCTIVE PERFORMANCE OF URBAN-NESTING SWAINSON'S HAWKS IN THE CENTRAL VALLEY OF CALIFORNIA

A. SIDNEY ENGLAND[1]

Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616 U.S.A.

JAMES A. ESTEP

Jones & Stokes Associates, 2600 V Street, Sacramento, CA 95818 U.S.A.

WALDO R. HOLT

3900 River Drive, Stockton, CA 95204 U.S.A.

ABSTRACT.—From 1990–94, we studied Swainson's hawks (*Buteo swainsoni*) nesting in the cities of Davis and Stockton and in adjacent rural habitats in California's Central Valley. We documented 31 urban nesting attempts at 16 sites in Davis and 34 nesting attempts at 24 sites in Stockton. Most were located in residential neighborhoods (Davis 81%, Stockton 71%) with the remainder in park-like landscapes or commercial/industrial settings. Nests were found more frequently in neighborhoods >20 yr old, with areas >45 yr old preferred due to the availability of mature landscaping. Three nests were found in neighborhoods <20 yr old, all in trees that predated urbanization. Nest trees were significantly taller than a random sample in 20–45-yr-old neighborhoods, but not in areas >45 yr old. Conifers were preferred over other trees in Davis (79%) and Stockton (94%) regardless of neighborhood age; conifers may provide better visual screening from below than other tree types. Fewer young fledged from nests in urban than in rural settings ($P < 0.05$). The proportion of nesting attempts resulting in at least one fledgling, and the number of young fledged per nesting attempt and per successful nest for urban nests were among the lowest reported for this species. Swainson's hawk nests have not been found in apparently suitable urban areas in the Central Valley where foraging habitat is unavailable for 5–8 km (e.g., Lodi and Sacramento), thus requiring long-distance transport of prey throughout the entire nesting cycle. Rapid urbanization or crop changes near cities could cause the long-term decline of Swainson's hawks in existing urban neighborhoods.

KEY WORDS: *Buteo swainsoni; California; nest-site selection; reproductive success; Swainson's hawk; urban-nesting.*

Selección del sitio de nidificación y características reproductivas de *Buteo swainsoni* urbano-nidificantes en el Valle Central de California

RESUMEN.—Desde 1990 a 1994, estudiamos individuos de *Buteo swainsoni* nidificantes en las ciudades de Davis y Stockton, además de hábitat rurales adyacentes en el Valle Central de California. Documentamos 31 nidos urbanos en 16 sitios localizados en Davis y 34 nidos en 24 sitios de Stockton. La mayoría de los nidos fueron localizados en vecindarios residenciales (81% en Davis y 71% en Stockton), el remanente se ubicó en paisajes parecidos a parques o en sitios cómerciales e industriales. Los nidos fueron encontrados más frecuentemente en vecindarios de más de 20 años de antiguedad, con áreas mayores a 45 años de antiguedad, preferidas debido a la disponibilidad de paisajes maduros. Tres nidos fueron encontrados en vecindarios con menos de 20 años de antiguedad y todos ubicados en árboles. Los árboles con nidos fueron significativamente más delgados que los obtenidos en una muestra azarosa en un vecindario de 20 a 45 años de antiguedad, pero no en áreas mayores a 45 años de edad. Las coníferas fueron preferidas sobre otros tipos de árboles en Davis (79%) y Stockton (94%) independientemente de la edad del vecindario; las coníferas proveen un mejor campo visual que otros tipos de árboles. El número de juveniles producidos en nidos urbanos era menor a los producidos en asentamientos rurales ($P < 0.05$). La proporción de nidificaciones resultantes en al menos un volantón y el número de juveniles por nidificación y por nido

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[1] Present address: Planning and Budget Office, University of California, Davis, CA 95616 U.S.A.

exitoso para nidos urbanos, se encuentra entre los más bajos reportados para esta especie. Nidos de *B. swainsoni* no han sido encontrados en áreas urbanas aparentemente apetecibles en el Valle Central, donde los hábitat de forrajeo no estan disponibles en 5 a 8 km (e.g., Lodi y Sacramento) asi necesitan transportar grandes distancias sus presas. La rápida urbanización o cambios en las cosechas cerca de las ciudades podría causar una declinación a largo plazo de *B. swainsoni* en los vecindarios urbanos existentes.

[Traducción de Ivan Lazo]

In their reviews of the biology of the Swainson's hawk (*Buteo swainsoni*), neither Bent (1937) nor Palmer (1988) reported nesting in an urban setting. The first documented record of urban-nesting Swainson's hawks was in a Fremont cottonwood (*Populus fremontii*) in Davis, California in 1979 (Peter H. Bloom pers. comm.). Subsequently, James (1992) reported five successful urban nests found between 1988 and 1991 in Regina, Saskatchewan.

The California Department of Fish and Game (CDFG) classifies the Swainson's hawk as a threatened species. To understand why this species has declined in California, considerable research has been focused on its population, nesting, and foraging ecology in the Central Valley (Bloom 1980, Schlorff and Bloom 1984, Estep 1989, Risebrough et al. 1989, and Babcock 1995). Recent surveys in the Central Valley have revealed that Swainson's hawks regularly nest in certain urban settings in Sacramento, San Joaquin, Solano, and Yolo counties. They are not known to nest regularly in urban settings in either the more northern or southern portions of the Central Valley.

From 1990 through 1994, we studied urban-nesting Swainson's hawks in two cities in the Central Valley—Davis (Yolo County) and Stockton (San Joaquin County)—and in the surrounding agricultural landscape. We wanted to answer three primary questions: (1) What nest-site characteristics are the hawks selecting by tree type, tree height, and age of the surrounding urban neighborhood? (2) Do they fledge as many young as hawks that select nest sites in agricultural habitats? and (3) Why do Swainson's hawks nest in some Central Valley communities and not in others?

STUDY AREAS AND METHODS

We monitored the reproductive performance of nesting Swainson's hawks on two study areas in the Central Valley of California from 1990 through 1994 (Fig. 1). The Yolo County area covered approximately 346 km², and more than 90% of it was in irrigated agriculture. The diverse mixture of crops was dominated by annual species including tomatoes, beets, grains, alfalfa, sunflower, and safflower. Orchards, vineyards and other perennial crops and also dry and irrigated pastures were <2% of the landscape. Native habitats were restricted almost exclusively to narrow bands of riparian vegetation along water courses, and small, isolated stands of valley oak (*Quercus lobata*). Two urban areas, Davis and Woodland, constituted approximately 5% of the study area and were surrounded by agricultural landscape.

The San Joaquin County study area covered approximately 390 km². Approximately 37% was urbanized land within Stockton, and the remainder was agricultural land (Fig. 1). The composition and diversity of crops were similar to the Yolo County study area. Native habitats also were limited to small, isolated stands of valley oak and riparian vegetation confined by flood control levees along stream courses.

Nest surveys were conducted each year from early April through June by inspecting all potential nesting habitat including nest sites occupied in previous years. Occupied nests were revisited at least once between mid-July and late August to count young fledged. Chicks reaching fledgling size were presumed to have fledged successfully (Steenhof and Kochert 1982). Nest sites were defined as urban if the nest was immediately adjacent to urban land uses and <250 ha of agricultural or undeveloped land was found within 1.5 km of the nest. The ages of neighborhoods in Davis were determined from 1952, 1975, and 1993 street maps and in Stockton from 1934, 1975, and 1993 street maps.

In 1994, we characterized existing trees in Davis at 198 points stratified by neighborhood age and spaced a minimum of 0.25 km apart. At each point, we recorded whether the nearest tree and the tallest tree within 50 m were conifers, and the height of the tallest tree within 50 m. The same data were recorded for all urban nest trees in Davis.

Nest productivity data were not distributed normally and could not be transformed for analysis with parametric statistical procedures. A one-tailed Wilcoxon matched-pairs signed-ranks test was used to compare nest productivity between rural and urban nests (Daniel 1990). The results of this nonparametric test were conservative because considerable information was lost by reducing the data to ranks of the annual differences in nesting success.

RESULTS AND DISCUSSION

The 31 urban-nesting attempts recorded from 1990–94 in Davis occurred at 16 different sites (Table 1). Similarly, the 34 urban-nesting attempts in Stockton occurred at 24 different sites. The most common setting (81% in Davis and 71% in Stockton) was in the yards of homes in residential neighborhoods (Fig. 2). In both cities, nests were also found
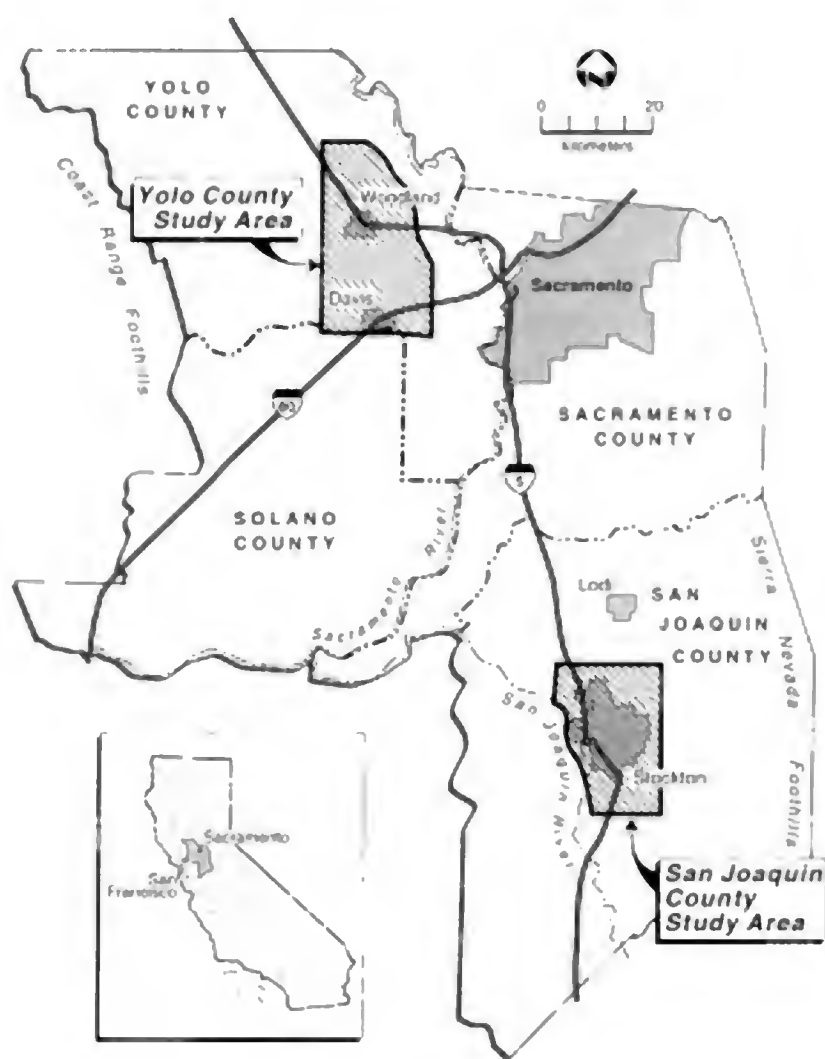
Figure 1. Location of the Yolo and San Joaquin study areas and urban centers in the Central Valley of California.

in park-like landscapes (19% in Davis and 17% in Stockton) such as golf courses, cemeteries, and on the central campus at the University of California, Davis. However, nests were notably absent from all urban parks. Three nests in Stockton were in commercial and industrial settings—two next to major intersections in commercial areas (Fig. 2), and one between State Highway 99 and the on- and off-ramps to the freeway. The settings for urban nest sites in the Central Valley were similar to those described by James (1992) in Regina, Saskatchewan. The level of human activity varied considerably between the sites, but was ongoing and highly predictable throughout the nesting season including during courtship and nest-site selection. Thus, urban-nesting Swainson's hawks selected sites with adjacent human activities and habituated to the setting from the beginning of the nesting cycle.

Nest-site Selection. Swainson's hawk nests in trees that postdated urbanization were found more frequently in neighborhoods >20 yr old than expected by chance in Davis (Fisher Exact Test, $P = 0.041$) and nearly so in Stockton (Fisher Exact Test, $P = 0.051$; Table 2). Neighborhoods >45 yr old were preferred, and nesting did not occur in neighborhoods <20 yr old except at three locations in Stockton where large, old trees that predated urbanization were used (Table 2). In Davis and Stockton, the

Table 1. Reproductive performance of urban- and rural-nesting Swainson's hawks in the Yolo and San Joaquin County study areas.

STUDY AREA/ YEAR	URBAN			RURAL		
	NESTING ATTEMPTS	SUCCESSFUL NESTS	YOUNG FLEDGED	NESTING ATTEMPTS	SUCCESSFUL NESTS	YOUNG FLEDGED
Yolo County (Davis urban nests)						
1990	6	5	9	68	64	109
1991	8	6	9	86	74	116
1992	5	2	3	116	94	143
1993	4	2	4	94	66	105
1994	8	7	11	128	106	190
Total	31	22	36	492	404	663
San Joaquin County (Stockton urban nests)						
1990	3	1	2	13	11	24
1991	5	3	3	12	9	11
1992	5	5	9	10	7	12
1993	9	5	8	9	7	14
1994	12	8	14	16	14	22
Total	34	22	36	60	48	83

Figure 2. Typical settings for urban Swainson's hawk nests: (A) Deodar cedar (*Cedrus deodara*) in a commercial/industrial neighborhood, Stockton, Calif.; (B) introduced pine (*Pinus* sp.) in a residential neighborhood, Davis, Calif.
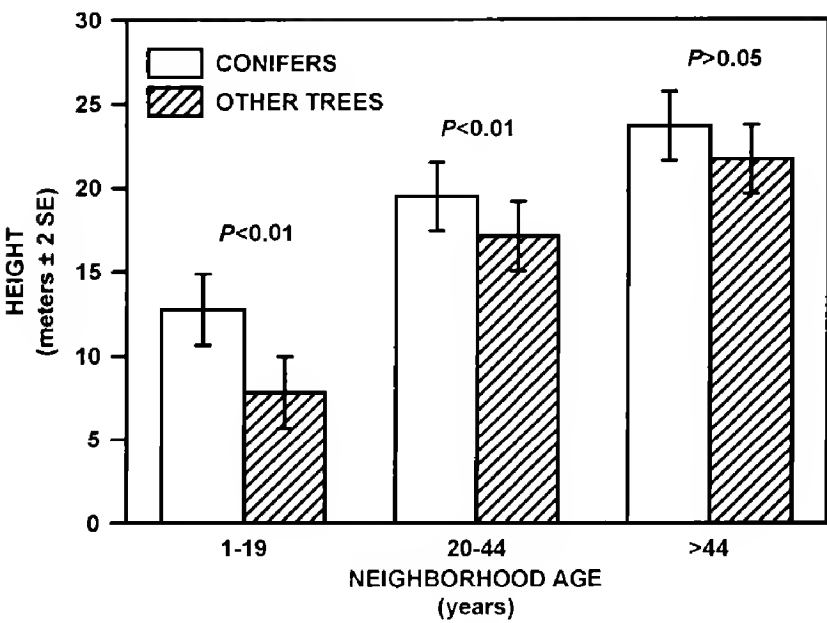
Figure 3. Height comparison from a random sample of the tallest trees stratified by tree type and neighborhood age in Davis, California. Significant effects were due to tree type, neighborhood age, and the interaction between these two variables (ANOVA, $F = 83.2$, $P < 0.001$).

proportion of nest trees that predated urbanization was inversely related to neighborhood age, with no preexisting trees used in neighborhoods >45 yr old. This pattern of nest tree selection is presumed to be related to the absence of potential nest trees of suitable size in younger neighborhoods. In 20–45-yr-old Davis neighborhoods, the mean height of nest trees (22.4 m) differed from a random sample of the

Table 2. Distribution of nest trees used by urban-nesting Swainson's hawks in Davis and Stockton, California, compared with age and size of neighborhoods.

City/ Neighbor- hood Age	Area (ha)	Nest Trees	Pre- existing Nest Trees[a]
Davis			
≤1951	300 (9.9%)[b]	5 (31.3%)[b]	0%
1952–75	1585 (52.3%)	11 (68.8%)	18%
1976–94	1143 (37.8%)	0 (0.0%)	—
Total	3028	16	
Stockton			
≤1934	3494 (24.4%)	11 (45.8%)	0%
1935–75	7464 (52.1%)	10 (41.7%)	40%
1976–94	3364 (23.5%)	3 (12.5%)	100%
Total	14 322	24	

[a] Percentage of nest trees older than the age of the neighborhood.
[b] Percent of the total area.

Table 3. Proportion of urban nests placed in conifers compared to random samples drawn from all trees and the tallest trees in different age neighborhoods in Davis, California.

| Neigh- borhood Age | Proportion in Conifers | | |
	Nest Trees	All Trees[a]	Tallest Trees[a]
<1950	1.00	0.03[c]	0.37[c]
1951–75[b]	0.67	0.27[d]	0.56[e]
1976–94	—	0.20	0.38

[a] Binomial test comparison to proportion of nest trees.
[b] Excludes two nests in trees that predated development.
[c] $P < 0.01$.
[d] $P < 0.05$.
[e] $P > 0.05$.

tallest (18.7 m; $t = 2.77$, $P < 0.01$), indicating that Swainson's hawks selected the tallest trees in intermediate age neighborhoods. In neighborhoods >45 yr old, this comparison was 24.1 m versus 22.4 m ($t = 0.75$, $P > 0.46$), indicating no significant difference between the height of trees that were selected by Swainson's hawks and a random sample of the tallest trees.

Outside urban areas in the Central Valley, most Swainson's hawk nests have been reported in Fremont cottonwood or valley oak (Schlorff and Bloom 1984, Estep 1989). Urban nests that postdated urbanization were primarily in conifers in Davis (79%) and Stockton (94%). In Davis, conifers were selected more frequently than expected based on their relative abundance in the urban landscape (Table 3). Conifers were taller than other trees in neighborhoods <45 yr old (Fig. 3) suggesting the preference may be for the tallest trees and not specifically for conifers. However, in neighborhoods >45 yr old, conifers were not significantly taller than other tree types (Fig. 3), but Swainson's hawks' nests were found in conifers more frequently than expected based on conifer abundance (Table 3).

James (1992) noted that three of four nest trees in Regina, Saskatchewan, were in conifers. He stated this pattern was opposite of that found in more typical habitats (Schmutz et al. 1980 and Bechard et al. 1990). However, Swainson's hawks will nest in conifers if present. Bechard et al. (1990) provided an unranked list of nest trees that included ponderosa pine (*Pinus ponderosa*) and western juniper (*Juniperus occidentalis*). Bloom (1980) reported that most

Swainson's hawk nests were found in junipers (*Juniperus* sp.) in the Great Basin portion of northeastern California. In the Central Valley, conifers were present only in urban settings and around some farmhouses. We speculate that Swainson's hawks prefer conifers in urban settings because the dense foliage and radial branching pattern provide more complete visual screening from human activities below the nest than trees with leaves only near branch tips and a dendritic branching pattern.

Reproductive Performance. Urban-nesting Swainson's hawks in the Yolo County study area fledged fewer young per nesting attempt each year than rural-nesting hawks (Fig. 4). The same relationship was observed in 4 of 5 yr in the San Joaquin County study area (Fig. 4). Analysis of these patterns using a one-tailed Wilcoxon matched-pairs signed-ranks test showed a significant difference in Yolo County ($T_- = 0$, $P < 0.05$) but not in San Joaquin County ($T_- = 3$, $P = 0.16$). However, five was the minimum sample size required for this nonparametric test, and the number of young fledged needed to be lower for urban nests in all 5 yr to yield a significant difference. The inability to confirm statistical significance for Stockton was likely a result of small sample size. Pooling the results from the two study sites also showed that fewer young were fledged from nests in urban settings ($T_- = 7$, $P < 0.05$).

The proportions of successful nests (those that fledged at least one young) in both Davis and Stockton were lower than on adjacent rural lands, and among the lowest when compared to other reported
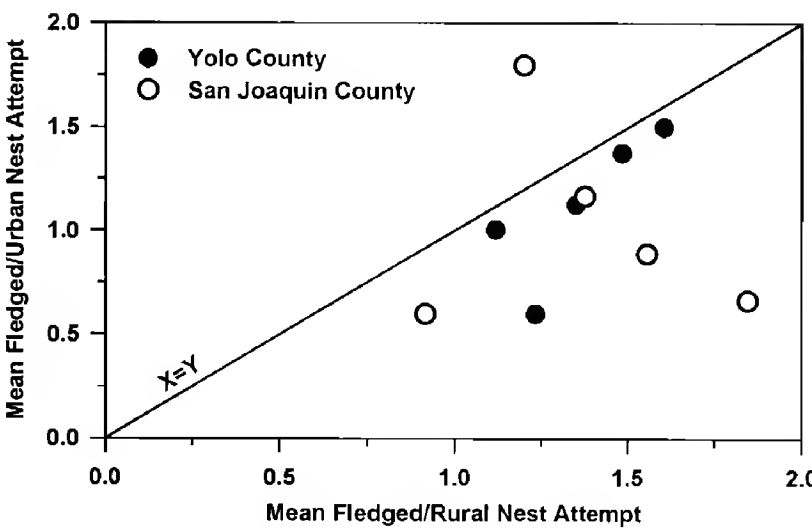

Figure 4. Mean number of young fledged, 1990 through 1994, from urban and rural nests in the San Joaquin and Yolo County study areas. Diagonal line indicates equal reproductive success at urban and rural nest sites.

multi-year studies (Table 4). The number of young fledged per nesting attempt and per successful nest for urban nests were also among the lowest reported values. Rural nests in Yolo and San Joaquin counties had similar success rates and number of young fledged per nesting attempt compared with other studies. However, the number of young per successful rural nest was similar to urban nests and lower than values reported at other locations.

Nesting in Other Central Valley Towns. Swainson's hawks also nest in the older neighborhoods of several major urban areas in the Central Valley portions of Sacramento, San Joaquin, Solano, and Yolo counties (Table 5). They are conspicuously absent, however, from the City of Lodi and the Sac-

Table 4. Reproductive performance of Swainson's hawks outside California compared to reproductive performance of Swainson's hawks in the Yolo and San Joaquin County study areas. All studies conducted for at least 3 yr.

LOCATION	YEARS	NEST ATTEMPTS	SUCCESSFUL NESTS (%)	FLEDGED/ ATTEMPT	FLEDGED/ SUCCESSFUL	SOURCE
SE Washington	3	48	81.3	1.50	1.85	Fitzner (1978)
NE Colorado	3	119	54.6	1.19	2.18	Olendorff (1978)
SE Alberta	3	153	71.2	1.41	1.98	Schmutz et al. (1980)
SE Washington	5	96	—	1.11	—	Bechard (1983)
SE New Mexico	3	36	81.0	1.67	1.94	Bednarz (1988)
Yolo County[a]	5	492	82.1	1.35	1.64	This study
San Joaquin Co.[a]	5	60	80.0	1.38	1.73	This study
City of Davis[b]	5	31	70.9	1.16	1.64	This study
City of Stockton[b]	5	34	64.7	1.06	1.64	This study

[a] Rural nest sites.

[b] Urban nest sites.

Table 5. Breeding status of urban-nesting Swainson's hawks in major urban areas in the Central Valley portion of Sacramento, San Joaquin, Solano, and Yolo Counties, California.

CITY	1993 POPULATION[a]	URBAN-NESTING SWAINSON'S HAWKS?
Woodland	41 850	Yes
Davis	50 100	Yes
Lodi	53 700	No
Stockton	226 300	Yes
Sacramento[b]	1 068 900	Urban edge only

[a] California Department of Finance 1993.

[b] Sacramento metropolitan area.

ramento metropolitan area. Numerous field surveys ranging from CDFG-sponsored efforts to environmental assessments have failed to detect urban-nesting Swainson's hawks in either of these locations. Both communities were established before the turn of the century and have old neighborhoods with apparently suitable habitat for urban nests.

Besides providing suitable nesting habitats, the cities that support urban-nesting Swainson's hawks are surrounded by crops that are suitable Swainson's hawk foraging habitat. However, Lodi is nearly surrounded by vineyards for 8–10 km, a crop type not used for foraging by Swainson's hawks (Estep 1989). The older neighborhoods of Sacramento are similarly encompassed by at least 5–8 km of urban development. Swainson's hawks do nest in Sacramento, but are limited to a narrow band of riparian vegetation along the Sacramento River. Along most of its course through the city, the Sacramento River is at the interface between urban development and agricultural lands, and these nests are adjacent to suitable foraging habitat.

Estep (1989) and Babcock (1995) have shown that Swainson's hawks in the Central Valley of California will forage more than 15 km from a nest site. While these distant sites may be critical at times, long-distance foraging bouts are generally limited to periods when suitable foraging habitat is not available nearby due to crop phenology. Babcock (1995) observed prey caught at long distances from nest sites frequently was consumed by adult birds near the point of capture. Prey brought back to the nest to provision young or a mate was generally caught near the nest. Presumably this pattern is due to the energetic inefficiency of transporting prey long dis-

tances. Similarly, Swainson's hawks are extremely rare in the northern and southern portions of the Central Valley where potential nest sites in urban and rural settings are surrounded by vineyards, orchards, rice, and cotton, all unsuitable Swainson's hawk foraging habitat (Estep 1989). The energetic cost of transporting prey these distances throughout the nesting cycle apparently is too great.

Land Use Changes and Urban Nesting. As urbanization continues in the Central Valley, the availability of Swainson's hawk foraging habitat will decline and the remaining foraging habitat will be at greater distances from older neighborhoods with suitable nest sites. These two trends will typically increase the distance between foraging areas and urban nest trees. Thus, the energetic costs of nesting will increase and reproductive success may decline. The only foreseeable change counteracting these trends is that newer neighborhoods will mature and may become nesting habitat. If urban expansion occurs too quickly, urban-nesting birds may be lost as the distance from nest sites to foraging habitat becomes too great, typically >5–8 km in the study area. If the mixture of agricultural crops next to cities such as Davis or Stockton becomes less suitable for foraging, urban-nesting birds could be expected to decline if the distance to foraging habitat becomes too great. Agricultural land uses are typically dictated by market conditions and are not as easily predictable as future urbanization.

Why Urban Nesting? Why do Swainson's hawks nest in urban settings where reproductive success is lower? Two alternative hypotheses could explain this paradox. First, rural nesting habitat may be saturated. Competition for nest sites could force some birds into the less productive, urban habitat. This hypothesis is consistent with the observation that the highest concentrations of Swainson's hawks in the Central Valley are in Sacramento, San Joaquin, Solano, and Yolo counties (Bloom 1980, Estep 1989). However, a portion of rural nest sites are unoccupied each year. In neither study area was the number of urban nesting attempts correlated with the number of rural nesting attempts. This relationship might be expected if birds were forced into urban settings when the number of rural nest attempts was high. Second, reproductive success might be comparable or better in urban than in rural settings if parameters such as lifetime reproductive success or post-fledging survival are considered. For example, if the mortality of adults in urban settings is lower due to decreased

predation or a lower likelihood of being shot, then the expected lifetime reproductive success would be higher.

LITERATURE CITED

BABCOCK, K.W. 1995. Home range and habitat use of breeding Swainson's hawks in the Sacramento Valley of California. *J. Raptor Res.* 29:140–154.

BECHARD, M.J. 1983. Food supply and the occurrence of brood reduction in Swainson's hawk. *Wilson Bull.* 95:233–242.

BECHARD, M.J., R.L. KNIGHT, D.G. SMITH AND R.E. FITZNER. 1990. Nest sites and habitats of sympatric hawks (*Buteo* spp.) in Washington. *J. Field Ornithol.* 61:159–170.

BEDNARZ, J.C. 1988. A comparative study of the breeding ecology of Harris' and Swainson's hawks in southeastern New Mexico. *Condor* 90:311–323.

BENT, A.C. 1937. Life histories of North American birds of prey. U.S. Natl. Mus., Bull. No. 176. Washington, DC U.S.A.

BLOOM, P.H. 1980. The status of the Swainson's hawk in California, 1979. Wildlife Management Branch, Nongame Wildl. Invest., Job II-8.0. Calif. Dept. Fish and Game, Sacramento, CA U.S.A.

CALIFORNIA DEPARTMENT OF FINANCE. 1993. California statistical abstracts. California Department of Finance, Sacramento, CA U.S.A.

DANIEL, W.W. 1990. Applied nonparametric statistics. PWS-KENT Publ. Co., Boston, MA U.S.A.

ESTEP, J.A. 1989. Biology, movements, and habitat relationships of the Swainson's hawk in the Central Valley of California, 1986–87. Calif. Dept. Fish and Game, Nongame Bird and Mammal Sec. Rep., Sacramento, CA U.S.A.

FITZNER, R.E. 1978. Behavioral ecology of the Swainson's hawk (*Buteo swainsoni*) in southeastern Washington. Ph.D. dissertation. Washington State Univ., Pullman, WA U.S.A.

JAMES, P.C. 1992. Urban-nesting of Swainson's hawks in Saskatchewan. *Condor* 94:773–774.

OLENDORFF, R.R. 1978. Population status of large raptors in northeastern Colorado–1970–1972. *Raptor Res. Rep.* 3:185–205.

PALMER, R.S. 1988. Handbook of North American birds. Vol. 5, Diurnal raptors, Part 2. Yale Univ. Press, New Haven, CN U.S.A.

RISEBROUGH, R.W., R.W. SCHLORFF, P.H. BLOOM AND E.E. LITTRELL. 1989. Investigations of the decline of Swainson's hawk populations in California. *J. Raptor Res.* 23:63–71.

SCHLORFF, R.W. AND P.H. BLOOM. 1984. Importance of riparian systems to nesting Swainson's hawks in the Central Valley of California. Pages 612–618 *in* R.E. Warner and K.M. Hendrix [EDS.], California riparian systems: ecology, conservation, and productive management. Univ. California Press, Berkeley, CA U.S.A.

SCHMUTZ, J.K., S.M. SCHMUTZ AND D.A. BOAG. 1980. Coexistence of three species of hawks (*Buteo* spp.) in the prairie-parkland ecotone. *Can. J. Zool.* 58:1075–1089.

STEENHOF, K. AND M.N. KOCHERT. 1982. An evaluation of methods used to estimate raptor nesting success. *J. Wildl. Manage.* 46:885–893.

REPRODUCTIVE PERFORMANCE, AGE STRUCTURE, AND NATAL DISPERSAL OF SWAINSON'S HAWKS IN THE BUTTE VALLEY, CALIFORNIA

BRIAN WOODBRIDGE

USDA Forest Service, Klamath National Forest, 1312 Fairlane Road, Yreka, CA 96097 U.S.A.

KAREN K. FINLEY

31338 S.W. Bellfountain Road, Corvallis, OR 97333 U.S.A.

PETER H. BLOOM

Western Foundation of Vertebrate Zoology, 439 Calle San Pablo, Camarillo, CA 93010 U.S.A.

ABSTRACT.—We monitored annual occupancy, reproductive performance, and natal dispersal of a marked population of Swainson's hawks (*Buteo swainsoni*) from 1984–94. Annual territory occupancy varied from 61–90%. Mean annual nest success was 65% (SE = 3.4%), and annual fledging rate was 1.53 (SE = 0.14) young per nest attempt. Of 567 Swainson's hawks banded as nestlings during this study, 41 were later recaptured as breeding adults. Mean age at recapture was 5.9 yr (SE = 0.37; range = 3–15 yr. The mean age of color-marked adults observed in either 1993 or 1994 was 8.2 yr (SE = 0.52), and ranged from 4–15 yr. Dispersal distances from natal site to subsequent breeding site ranged from 0–18.1 km (mean = 8.2 km, SD = 3.1), and was not different from random distances among territories.

KEY WORDS: *Buteo swainsoni*; *dispersal*; *mark-recapture*; *population demography*; *Swainson's hawk*; *territory occupancy*.

Características reproductivas, estructura de edad y dispersion natal *Buteo swainsoni* en el Butte Valley, California

RESUMEN.—Desde 1984 a 1994, monitoreamos la ocupación anual, características reproductivas y dispersión natal de una población marcada de *Buteo swainsoni*. La ocupación de territorio varió anualmente desde un 61 a un 90%. La media anual de éxito del nido fue de un 65% (EE = 3.4). La tasa anual de polluelos fue de 1.53 (EE = 0.14) juveniles por nidificación. De 567 individuos marcados como polluelos durante este estudio, 41 fueron recapturados como adultos reproductivos. La edad media de recaptura fue de 5.9 años (EE = 0.37; rango = 3–15 años). La edad media de adultos marcados 1993 o 1994 fue de 8.2 años (EE = 0.52) con un rango de 4 a 15 años. Las distancias de dispersión entre el sitio natal y el posterior sitio reproductivo estaban en el rango de 0 a 18.1 km (media = 8.2 km; EE = 3.1) y no fue diferente a una distancia azarosa entre territorios.

[Traducción de Ivan Lazo]

Declines in numbers of Swainson's hawks (*Buteo swainsoni*) in California (Bloom 1980, Risebrough et al. 1989), Nevada (Oakleaf and Lucas 1976, Herron and Lucas 1978) and Oregon (Littlefield et al. 1984) have stimulated concern over long-term viability of this species' populations in the western United States. Numerous factors have been suggested as causes of regional declines, including loss of nesting habitat (Schlorff and Bloom 1983), conversion of foraging habitat to agriculture (Bloom 1980, Schmutz 1984, Estep 1989), livestock grazing (Littlefield et al. 1984, Woodbridge 1991), predation and interspecific competition (Littlefield et al. 1984,

Janes 1987) and environmental contaminants (Henny and Kaiser 1979, Risebrough et al. 1989). Increased mortality during the nonbreeding season, when the bulk of the North American population migrates to South America, has also been suggested as a potential cause of noted declines (Bloom 1980, White et al. 1989).

Neither causes nor remedies for population declines can be addressed without broad understanding of species biology and assessment of long-term patterns in population dynamics. Estimation of demographic parameters allows for analysis of population viability and trends, effects of management actions,

identification of critical life history stages, and comparisons with other populations (Noon et al. 1992). Such baseline data have proven essential in conservation of threatened and endangered species (Thomas et al. 1990, Noon et al. 1992).

We describe patterns of territory density, occupancy, productivity, age structure and dispersal in a population of Swainson's hawks over an 11-yr period, and discuss variability in these estimates. This study is part of a long-term investigation of the ecology and demography of Swainson's hawks in northern California.

STUDY AREA

This study took place in the Butte Valley in northern California, approximately 10 km south of the Oregon border and the Klamath Basin. The Butte Valley is included in the Modoc Plateau region of the California sagebrush steppe ecological province (Barbour and Major 1977) and is part of the basin and range physiographic province (Franklin and Dyrness 1973). The study focused primarily on the unforested floor of the Butte Valley, which ranges from 1280–1340 m in elevation and is approximately 415 km² in extent. Topography, soils, and natural vegetation of the Butte Valley are typical of the basin and range physiographic province (Franklin and Dyrness 1973). Dominant vegetative associations are western juniper (*Juniperus occidentalis*) woodland (22%), grazed sagebrush steppe (21%), wetlands and seasonally flooded areas (5%), and agricultural fields (53%). Cultivated crops include irrigated alfalfa (*Medicago sativa*), grains, and potatoes.

METHODS

We estimated the size and distribution of the breeding Swainson's hawk population in the Butte Valley by conducting systematic surveys of the valley floor each year from 1983–94. Surveys in the adjacent Klamath Basin consisted of visits to previously known territories. Open, flat terrain and high road densities in agricultural areas permitted good visibility and survey coverage from vehicles. Sage-steppe and juniper woodland habitats were surveyed on foot and from vehicles. In addition to searching for nest sites, we observed any foraging hawk of unknown origin until it returned to a nest site. Survey effort was concentrated during courtship and nest building (mid-April through late May) although new nests were located as late as August.

We defined a territory as an area containing an active nest and defended by a single pair of Swainson's hawks in at least one year. In subsequent years, territories were classified as occupied if at least one adult was observed repeatedly during the early nesting season. A pair was considered to have attempted to breed if a nest was constructed or new material added to an existing nest. Deserted nests were included in the sample if they showed signs of use in the present year (Postupalsky 1974, Steenhof and Kochert 1982). The number of nestlings and unhatched or broken eggs was recorded during at least two nest checks, the first occurring about 1 wk after the mean hatching date (16 June) and the second at banding (4 July to 15 August). We considered a breeding attempt to be successful if ≥1 young survived to 5 wk of age. Pairs that built nests but did not breed were included with failed attempts.

To control bias associated with survey timing, lower detectability of failed breeding attempts (Steenhof and Kochert 1982), and to account for permanently abandoned nests discovered in early years of the study, we included only territories which had been occupied at least once during the four previous years in calculations of annual occupancy, nest success, and productivity. The exclusion of newly discovered territories from the annual calculations of annual success and productivity may result in a bias toward traditionally occupied territories with older breeders.

We banded nestling Swainson's hawks in the Butte Valley each year from 1980–94. We also marked breeding adults at the nest site by using a mist net with a live great horned owl (*Bubo virginianus*) as a decoy (Hamerstrom 1963, Bloom 1987). Adult hawks were marked with individually numbered plastic legbands and U.S. Fish and Wildlife Service lock-on aluminum bands. Searches for marked individuals were made each year at all known occupied territories, as well as along established transects in foraging habitats. Mean values in the text are presented with standard errors.

RESULTS AND DISCUSSION

Population Size and Density. Swainson's hawks occupying the Butte Valley during the breeding season were almost exclusively territorial adults; we recorded few nonterritorial adult floaters or subadults during the study. The high frequency of marked individuals (80% of breeders in 1994) in the population enabled us to distinguish nonbreeding floaters from territorial pairs and nonterritorial failed breeders.

The number of Swainson's hawk territories monitored during this study increased from 12 in 1984 to 83 in 1994. (Not all of these are included in calculations of reproductive parameters.) Increases during the earlier years of the study were due to improved survey coverage; after 1990, however, fluctuations were related to colonization of new sites and abandonment of traditional territories. Since 1990, 14 new territories were established within the study area, and four traditional territories were abandoned. The dependence of Butte Valley Swainson's hawks on limited high-quality foraging habitats such as sprinkler-irrigated alfalfa was expressed in the locations of newly colonized territories. Twelve of the 14 new territories were established near fields that had recently been converted to alfalfa cultivation.

Table 1. Annual occupancy, nest success, and fledging rate for Swainson's hawk territories in the Butte Valley, California, 1984–94.

YEAR	N TERRI-TORIES[a]	PERCENT OCCUPIED	PERCENT SUCCESS-FUL	MEAN NUMBER OF YOUNG FLEDGED PER NEST ATTEMPT (SE)
1984	12		66.7	1.25 (0.37)
1985	13	77	60.0	1.30 (0.40)
1986	22	91	80.0	2.00 (0.26)
1987	34	88	73.3	1.71 (0.23)
1988	38	84	71.9	1.80 (0.20)
1989	45	84	65.8	1.30 (0.20)
1990	56	84	78.7	2.00 (0.20)
1991	64	86	52.7	1.50 (0.20)
1992	66	73	47.9	0.79 (0.14)
1993	64	61	51.3	1.10 (0.15)
1994	73	74	72.2	2.20 (0.15)
Mean		80.2	65.5	1.53
SE		2.8	3.4	0.14

[a] Number of territories sampled.

Most nests were located in western junipers, although four nests were constructed in ponderosa pine (*Pinus ponderosa*), one in an elm (*Ulmus* sp.), two in basin bigsage (*Artemisia tridentata*). Territory distribution was strongly affected by the availability of patches of western juniper in close proximity to agricultural habitats used for foraging (Woodbridge 1991).

Overall territory density was 20/100 km². Territory density varied among five large (50–150 km²) landscape blocks, ranging from 5.7/100 km² in irrigated pasture to 36.8/100 km² in a landscape dominated by alfalfa cultivation.

Territory Occupancy. The proportion of territories occupied in a given year ranged from 91% in 1986 to 61% in 1993, averaging 80% (SE = 2.8) over all years (Table 1). Fluctuations in annual occupancy rates were caused by non-use of traditional territories and by new pairs attempting to establish territories in previously unoccupied areas. Occupancy also varied among individual territories, ranging from 14–90% of years monitored. At 52 territories with more than five consecutive years of monitoring data, we identified 35 traditional territories that were occupied during most (>50%) years of the study. Seventeen ephemeral territories exhibited low (≤50%) occupancy rates.

Reproductive Success. Between 1984 and 1994 we observed 454 nest attempts. Overall, pairs were successful in 65% (SE = 3.6) of reproductive attempts, with annual success ranging from 48–80% (Table 1). Success rates were significantly lower during the period from 1991–93. Nesting failure between 1986 and 1990 typically resulted from loss of nestlings (51% of failures), failure to lay eggs (24%), failed incubation (17%) and incomplete nest-building (8%; Woodbridge 1991). Known nestling losses that resulted in nest failure were caused by starvation ($N = 21$), predation by great horned owls ($N = 5$) or golden eagles (*Aquila chrysaetos*) ($N = 2$), windstorms ($N = 5$) and human disturbance ($N = 3$).

Fledging Rate. The mean fledging rate for all nest attempts was 1.53 (SE = 0.14) young per nest attempt, ranging from 0.79 (SE= 0.14) in 1992 to 2.20 (SE = 0.15) in 1994 (Table 1). Mean annual fledging rates varied among individual territories. Of 52 territories with more than five consecutive years of monitoring data, 11% exhibited low (<0.5 young/attempt) fledging rates; an additional 11% fledged <1.0 young/attempt. Fledging rates were >1.50 young/attempt at 42% of monitored territories. Territories with consistently low reproduction were associated with sage-steppe habitats, whereas agricultural habitats supported higher reproductive rates (Woodbridge 1991).

Mark-recapture Results. We banded 567 nestling Swainson's hawks in the Butte Valley between 1979 and 1994. Forty-one of these marked nestlings were recaptured as breeding adults in subsequent years, and nine were recovered as post-fledging mortalities within the Butte Valley. An additional eight were recovered in Latin America, giving an overall band return rate of 10.2%. The virtual absence of subadult Swainson's hawks in the study area, however, suggests that these birds spend their second summer elsewhere, and may not be available for recapture. This would result in underestimation of band return rates, which are largely based on recapture of breeding adults.

Population Age Structure. Swainson's hawks occupying the Butte Valley during the breeding season were almost exclusively in adult plumage; we recorded only 12 individuals in subadult plumage. Subadults observed early in the season (April to May) were typically absent after mid-May, and were assumed to be late migrants. Paired territorial Swainson's hawks in subadult plumage were re-
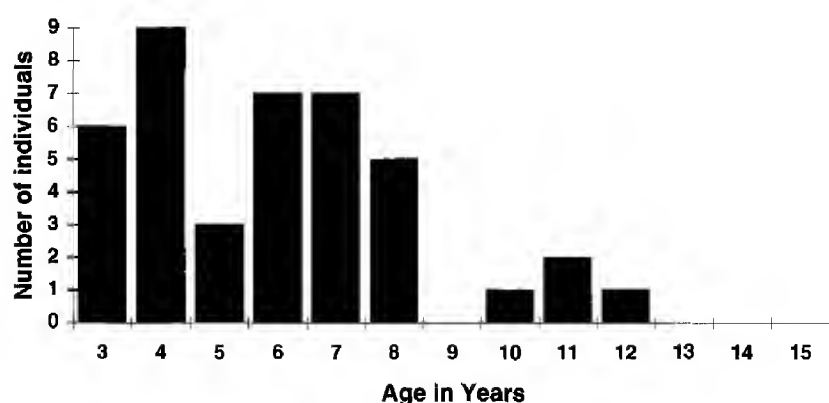
Figure 1. Frequency distribution of age at recapture of 41 Swainson's hawks banded as nestlings in the Butte Valley, California, 1980-94.
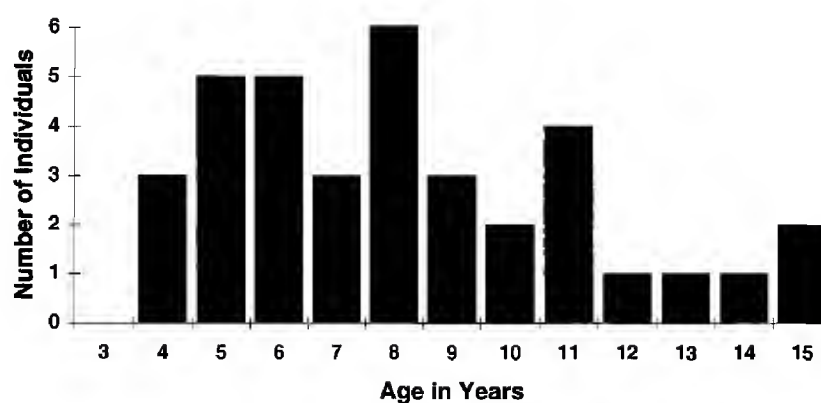

Figure 2. Frequency distribution of ages for 36 Swainson's hawks banded as nestlings in the Butte Valley, California (1980-92) and observed in 1993-94.

corded on four occasions; in all cases the subadult hawk was female. One subadult male acted as a nest helper, provisioning young at a nest also tended by an adult pair.

Forty-one Swainson's hawks banded as nestlings in the Butte Valley have been recaptured as breeders since 1981. The mean age at recapture was 5.9 yr (SE = 0.37), ranging from 3-12 yr (Fig. 1). Age at recapture should not be interpreted as age of first breeding; many of these individuals may have bred elsewhere or eluded capture for several years before recapture. Of five 3-yr-old Swainson's hawks recaptured as territorial breeders (assumed first breeding), two were still in subadult plumage, suggesting some variability in maturation rates.

Approximately 80% of the 41 recaptured and color-marked Swainson's hawks were observed at least once in subsequent years. The age distribution of color-marked birds observed in either 1993 or 1994 (N = 36) ranged from 4-15 yr, with a mean age of 8.2 yr (SE = 0.52; Fig. 2). We believe that this is our best estimate of the age distribution of the breeding population. Mortalities of known-age Swainson's hawks were caused by collision with a train (one 6-yr-old male) and probable collision with vehicle (one 15-yr-old male).

Dispersal. We used natal dispersal distances and interterritory movements of marked adult Swainson's hawks to assess immigration and emigration in this study area. For 41 nestlings recaptured as breeding adults (20 female, 21 male), dispersal distances ranged from 0-18.1 km, and averaged 8.8 km (SE = 1.1 km). Mean distance between natal and subsequent breeding sites was not statistically different from random interterritory distance ($t = 1.06$, $P = 0.17$, two-tailed), and did not differ between

sexes ($t = 1.33$, $P = 0.12$, two-tailed). Our estimate of dispersal distance may be biased low, since survey effort is not as extensive in the adjacent Klamath Basin. Two breeding adults recaptured in the Butte Valley had moved 10.2 km and 7.9 km from natal sites in the adjacent Klamath Basin. We recorded only one confirmed case of natal dispersal to a breeding territory outside of the Butte Valley; this bird was found breeding at a territory in the Klamath Basin, 36.8 km from its natal site. A nestling banded in 1982 was found injured in April 1988 in Diamond Valley, Nevada, 565 km southeast from its natal site. Another nestling banded in 1979 was found injured in August 1981, in Christmas Valley, Oregon, 160 km northeast of its natal site. Whether these hawks were breeding at their recovery sites is unknown.

Dispersal of hawks into the Butte Valley from natal sites in the Klamath Basin suggests that the Butte Valley is not a closed population, and there may be substantial genetic interchange with the Klamath Basin area. The two areas are likely interacting elements of one metapopulation. Territory occupancy and reproductive success, however, differed dramatically between the two areas during the same period. Bloom and Hawks (in Risebrough et al. 1989) reported <50% territory occupancy and <50% nest success in the Klamath Basin in the mid-1980s, considerably less than in the Butte Valley. Because of unequal levels of marking and monitoring in the two areas, we were unable to quantify the level of exchange.

Within the Butte Valley study area, we recorded 25 interterritory movements by marked adult Swainson's hawks (11 male, 14 female). These movements ranged from 0.97-6.3 km (mean = 2.2, SE = 0.23 km), and typically were short moves between neigh-

boring territories. Mean adult dispersal distance was significantly less than the mean nearest-neighbor distance (3.7 km, SE = 0.87) for the Butte Valley population (t = 6.77, P = 0.03, one-tailed). Of 36 adult hawks marked in the adjacent Klamath Basin between 1981 and 1988, none were observed within the Butte Valley.

While evidence of natal dispersal and individual movements to and from our study area are valuable preliminary data, assessments of immigration and emigration would be greatly enhanced by more comprehensive monitoring of breeding Swainson's hawks in the neighboring Klamath Basin. Among other things, this would help us assess the extent to which the Butte Valley serves as a source population for more marginal habitat areas to the north and east.

Concluding Remarks. Because Swainson's hawks are long-lived, description of population demography requires long-term study of marked populations in order to account for the effects of generation time and environmental variability (Newton 1979, Noon et al. 1992). Temporal variability in reproductive performance such as we have observed during the course of this study may or may not translate into long-term changes in the local Swainson's hawk population. Assessment of critical values may best be accomplished through mathematical modelling of population trends based on life history matrices.

Identification of conservation measures for maintaining the long-term viability of this population depends on analysis of the extent to which differences in reproductive success and nestling survival are habitat related. The presence of both traditional and marginal ephemeral territories in our study area suggested that a subset of territories contributed disproportionately to the long-term viability of the population. In our area, cultivated alfalfa appears to have become a critical habitat element (see Woodbridge 1991), replacing the productive native grasslands which were the original vegetation. Conservation measures that restore productive perennial grasslands and open shrubsteppe habitats on public lands and Conservation Reserve lands in the Butte Valley might ensure the resilience of Swainson's hawks to changes in agricultural ecomomics and practices.

LITERATURE CITED

BARBOUR, M.G. AND J. MAJOR. 1977. Terrestrial vegetation of California. John Wiley and Sons, New York, NY U.S.A.

BLOOM, P.H. 1980. The status of the Swainson's hawk in California, 1979. Final Report II-8.0, USDI Bur. Land Manage. and Fed. Aid in Restoration, Proj. W-54-R-12, Calif. Dept. Fish and Game, Sacramento, CA U.S.A.

———. 1987. Capturing and handling raptors. Pages 99–123 in B.A. Gerin Pendleton, B.A. Millsap, K.W Cline and D.A. Bird [EDS.], Raptor management techniques manual. Natl. Wildl. Fed., Washington, DC U.S.A.

ESTEP, J.A. 1989. Biology, movements, and habitat relationships of the Swainson's hawk in the Central Valley of California, 1986–1987. Calif. Dept. Fish and Game, Nongame Bird and Mammal Sec. Rep. Sacramento, CA U.S.A.

FRANKLIN, J.F. AND C.T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8. Corvallis, OR U.S.A.

HAMERSTROM, F. 1963. The use of great horned owls in catching marsh hawks. *Proc. Internat. Ornithol. Congr* 13:866–869.

HENNY, C.J. AND T.E. KAISER. 1979. Organochlorine and mercury residues in Swainson's hawk eggs from the Pacific Northwest. *Murrelet* 60:2–5.

HERRON, G.B. AND P.B. LUCAS. 1978. Population surveys, species distribution, and key habitats of selected nongame species. Nev. Dept. Fish and Game, Job Perform. Rep., Proj. W-43-R, Study 1, Jobs 1 and 2, Reno, NV U.S.A.

JANES, S.W. 1987. Status and decline of Swainson's hawks in Oregon: the role of habitat and interspecific competition. *Oreg. Birds* 13:165–179.

LITTLEFIELD, C.D., S.P. THOMPSON AND B.D. EHLERS. 1984. History and present status of Swainson's hawks in southeast Oregon. *Raptor Res.* 18:1–5.

NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD U.S.A.

NOON, B.R., K.S. MCKELVEY, D.W. LUTZ, W.S. LAHAYE, R.J. GUTIERREZ AND C.A. MOEN. 1992. Estimates of demographic parameters and rates of population change. Pages 175–186 in J. Verner, K.S. McKelvey, B.R. Noon, R.J. Gutierrez, G.I. Gould and T.W. Beck [TECH. EDS.], The California spotted owl: a technical

assessment of its current status. Gen. Tech. Rep. PSW-GTR-133. USDA For. Serv., Albany, CA U.S.A.

OAKLEAF, R.J. AND P. LUCAS. 1976. Population surveys, species distribution, and key habitats of selected nongame species. Nev. Dept. Fish and Game, Job Perform. Rep., Proj. W-53-R, Study 1, Jobs 1 and 2, Reno, NV U.S.A.

POSTUPALSKY, S. 1974. Raptor reproductive success: some problems with methods, criteria and terminology. Pages 21–31 *in* F.N. Hamerstrom, Jr., B.E. Harrell and R.R. Olendorff [EDS.], Management of raptors. Raptor Res. Found., Vermillion, SD U.S.A.

RISEBROUGH, R.W., R.W. SCHLORFF, P.H. BLOOM AND E.E. LITTRELL. 1989. Investigations of the decline of Swainson's hawk populations in California. *J. Raptor Res.* 23:63–71.

SCHLORFF, R.W. AND P.H. BLOOM. 1983. Importance of riparian systems to nesting Swainson's hawks in the Central Valley of California. Pages 612–618 *in* R.E. Warner and K.M. Hendrix [EDS.], California riparian systems. Univ. California Press, Berkeley, CA U.S.A.

SCHMUTZ, J.K. 1984. Ferruginous and Swainson's hawk abundance in relation to land use in southeastern Alberta. *J. Wildl. Manage.* 48:1180–1187.

STEENHOF, K. AND M.N. KOCHERT. 1982. An evaluation of techniques used to estimate raptor nesting success. *J. Wildl. Manage.* 46:885–893.

THOMAS, J.W., E.D. FORSMAN, J.B. LINT, E.C. MESLOW, B.R. NOON AND J. VERNER. 1990. A conservation strategy for the northern spotted owl. U.S. Government Printing Office, Washington, DC U.S.A.

WHITE, C.M., D.A. BOYCE AND R. STRANEK. 1989. Observations on *Buteo swainsoni* in Argentina, 1984. Pages 79–87 *in* B.-U. Meyburg and R.D. Chancellor [EDS.], Raptors in the modern world. World Working Group on Birds of Prey and Owls, Berlin, Germany.

WOODBRIDGE, B. 1991. Habitat selection by nesting Swainson's hawks: a hierarchical approach. M.S. thesis, Oregon State Univ., Corvallis, OR U.S.A.

HOME RANGE AND HABITAT USE OF BREEDING SWAINSON'S HAWKS IN THE SACRAMENTO VALLEY OF CALIFORNIA

KEITH W. BABCOCK

Michael Brandman Associates, 10423 Old Placerville Road, Suite 100, Sacramento, CA 95827 U.S.A.

ABSTRACT.—Four adult Swainson's hawks (*Buteo swainsoni*) were radiotagged along the Sacramento River in 1992. The mean home range (minimum convex polygon) was 4038.4 ha (40.4 km²). Core areas of intensive use (adaptive kernal) by nesting Swainson's hawks ranged from 25.9–82.2 ha. Individual hawks foraged as far as 22.5 km from the nest. In the Sacramento Valley, foraging ranges and total home range area were strongly influenced by agricultural patterns and cover types. Ruderal and fallow fields, grain crops, and safflower were the vegetative cover types that ranked highest in foraging use. The predominance of less suitable cover types within the study area may explain the relatively large home ranges exhibited by the Swainson's hawks in this study.

KEY WORDS: Buteo swainsoni; *foraging ecology*; *habitat use*; *home range*; *Swainson's hawk*.

Rango de hogar y uso del hábitat de *Buteo swainsoni* reproductivos en el Valle Sacramento de California

RESUMEN.—En 1992, cuatro individuos adultos de la especie *Buteo swainsoni* fueron radio-marcados a lo largo del Río Sacramento, California. La media de rango de hogar (polígono convexo mínimo) fue de 4038.4 ha (40.4 km²). Areas núcleo de uso intensivo por parte de *B. swainsoni* se encontraban dentro de un rango de 25.9 a 82.2 ha. Los individuos de *B. swainsoni* se alimentaban en sitios distantes hasta 22.5 km del nido. En el Valle Sacramento, los rangos de forrajeo y el área total de rango de hogar, fueron fuertemente influenciados por patrones agrícolas y tipos de cubierta vegetacional. Campos ruderales y abandonados, cosechas de granos y cártamo fueron los tipos de cubiertas vegetativa de mayor uso como sitios alimentarios. La predominancia de cubiertas vegetales menos utilizadas en el sitio de estudio pueden explicar el rango de hogar relativamente grande exhibido por esta especie.

[Traducción de Ivan Lazo]

The Swainson's hawk (*Buteo swainsoni*) was common historically throughout most of the lowland grassland and riparian communities that once occupied the Central Valley of California (Grinnell and Miller 1944). However, an estimated 90% decline of the breeding population of this species in recent years (Bloom 1980) resulted in the listing of the Swainson's hawk in California as a threatened species. The current breeding range of the Swainson's hawk in California is generally comprised of two populations, one located in the Great Basin area in the northeastern corner of the state, and the other, larger population located primarily in the middle portion of the Central Valley (the Sacramento Valley) near Sacramento (Bloom 1980).

Very little is known about the breeding home range and foraging habitat requirements of the Swainson's hawk in the Sacramento Valley. And yet, this region is home to the highest concentration of Swainson's hawks in the state (Bloom 1980). Previous studies suggest that home-range sizes can vary significantly in response to agriculture, changes in prey availability, and various farming practices (Bechard 1982, Estep 1989, Woodbridge 1991). Using radiotelemetry, I determined home-range sizes, core-use areas, and habitat use of a small population of nesting Swainson's hawks in the Sacramento Valley.

STUDY AREA

This study was conducted in an open rural area within the city of West Sacramento, bordered on the east by the Sacramento River and the city of Sacramento. Agricultural cropland, pastureland, and areas of non-native grassland comprised the majority of the open space areas in the region. Common crop types included wheat, corn, tomatoes, alfalfa, onions, sugar beets, and safflower. Dense urban areas associated with West Sacramento and Sacramento occured to the north and east of the study area. Narrow riparian areas dominated by Frémont cottonwood (*Populus fremontii*), valley oak (*Quercus lobata*), walnut (*Juglans* sp.), willow (*Salix* sp.), and box elder (*Acer negundo*) occur along the Sacramento River to the east and along Putah Creek to the west. Isolated oak woodlands occur sporadically throughout the residential and agricultural areas.

METHODS

Swainson's hawks were trapped using dho-gazas (Hamerstrom 1963). A bal-chatri trap (Berger and Mueller 1959) and a noose carpet (Collister 1967) were used for a pair of Swainson's hawks that avoided the dho-gaza. All captured Swainson's hawks were weighed, sexed (determined by the presence or absence of a brood patch and by overall size and weight), and fitted with backpack transmitters weighing from 19.2–19.8 g. Radio signals were received using ICOM IC-03AT transceivers and three-element Yagi antennas. Each trapped hawk was also fitted with a numbered, colored plastic leg band and a standard U.S. Fish and Wildlife Service aluminum leg band.

Tracking began after each bird was fitted with a transmitter and released. In the Sacramento Valley, Swainson's hawks often congregate in large groups and begin migrating southward in September (Bloom 1980, Estep 1989). Tracking was discontinued on 31 August since home range and foraging information obtained after this period was not expected to be strongly correlated with nest territories. Each bird was followed from dawn until dusk at least 2 d/wk during the study period (1 June to 31 August).

Because of the very active and aerial nature of Swainson's hawks, these birds are regularly lost to view during periods of high-altitude soaring and straight flight. Data were recorded in 5-min intervals and only when the bird was visually observed. Behavioral information was recorded in terms of foraging or nonforaging. Foraging behavior included circling, hovering, stooping, and feeding. Nonforaging behavior included straight flight, perching (unless, because of location and habitat, it was considered foraging from a perch), incubating, and preening. Location points were plotted on aerial photographs containing field numbers for each cover type.

A geographic information system (GIS) was used to map land uses and observational points within the study area. Information associated with each observation (time, date, hawk number, vegetation type, behavior) were also incorporated into the database. Home range calculations for each radio-marked Swainson's hawk were later imported into the GIS database in order to create home-range polygons. These polygons were then overlain onto the study area map to enable analysis of hawk foraging habitat and to compare individual home ranges.

To avoid autocorrelation of data, only observations separated by at least 0.5-hr intervals were used to determine home ranges and habitat use. Lair (1987) suggested that observation points may be considered biologically independent if sufficient time has passed for the animal to have moved to a new location or, for the purposes of this study, to cross its home range. For this study it was estimated that it would take a Swainson's hawk no more than 0.5 hr to cross its home range.

Home ranges were calculated using the CALHOME program developed by J. Kie (unpubl.), and were based on field observations and locations plotted over the entire duration of the study. The home range of each hawk was determined using the minimum convex polygon (MCP) method. Because use of this method includes outlier location points (occasional or isolated movements to locations outside the normal use area) which tend to overestimate home-range sizes, a 95% contour level was used in order to exclude these points. A 50% contour level using the adaptive kernal (AK; Worton 1987) method was used for delineating core-habitat-use areas (those land areas that are used most extensively by nesting hawks as foraging habitat) within the home range. Core-use areas at the 50% MCP level were also determined for comparison.

To evaluate habitat use, information on the vegetative cover type or crop type at each Swainson's hawk observation point was also recorded. A chi-square analysis was used to compare Swainson's hawk habitat use with habitat availability.

RESULTS

Four adult Swainson's hawks, three males and one female (which was mated to one of the males), were trapped and radiotagged (Table 1). Attempts were made to trap all adults from the six pairs in the study area. The first hawk was trapped on 2 June 1992, and the last was trapped on 10 July 1992. Each radio-tagged hawk was tracked for an average of 138 hr over the duration of the study. The number of biologically independent points for each hawk ranged from 73–122.

Home Range and Core-Use Areas. Home ranges of the four radio-tagged hawks were relatively large (Table 1). At the 95% MCP contour level, home ranges varied from 723.6–7658.8 ha ($\bar{x}$ = 4038.4 ha, SD = 5348.4 ha, N = 4) and were linear in nature (Fig. 1). Home ranges of the three males were larger than that of the female, and averaged 5143.3 ha. The furthest any individual hawk foraged from the nest was 22.5 km.

The size (50% AK) of the core-habitat-use areas ranged from 25.9–82.2 ha ($\bar{x}$ = 48.2 ha, SD = 21.8 ha, N = 4) (Table 1). These core areas were generally located in the immediate vicinity of each nest. For comparison, mean core-use areas using the MCP technique was 86.5 ha (Table 1).

Habitat Use. Dominant cover types within the home ranges (100% MCP) of the radio-tagged Swainson's hawks were grain crops (17.4% of the total undeveloped land potentially available as Swainson's hawk foraging habitat), ruderal/fallow fields (16.3%), row crops (corn/milo/sudan grass; 10.9%), tomatoes (10.6%), and safflower (10.2%). When observed habitat use by the radio-tagged Swainson's hawks was compared to habitat availability, Swainson's hawks did not forage in a habitat in proportion to its availability, but were observed most often foraging over ruderal/fallow fields, alfalfa, and pastureland (χ^2 = 31.3, df = 11, P < 0.001).

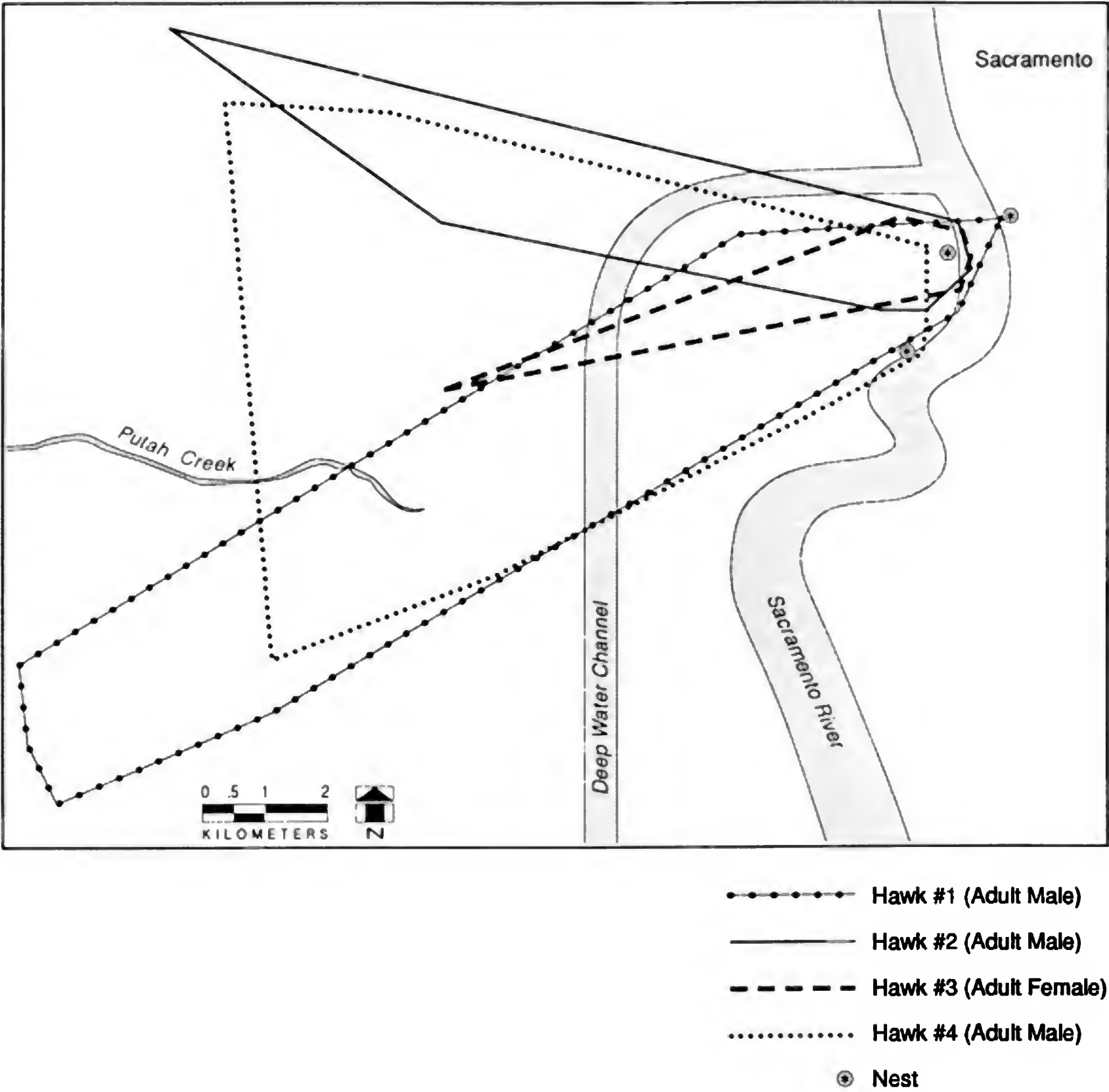**Foraging Behavior.** Both sexes of the radio-tagged

Figure 1.   Nest locations and home range sizes (95% MCP) of four radio-tagged Swainson's hawks in the Sacramento Valley of California. Hawks #2 and #3 were mates.

Swainson's hawks were observed foraging almost exclusively from the air. The hawks were highly active and never spent much time over a particular field unless attracted by cutting or harvesting activities. In some instances, particularly in late July and August, large groups of Swainson's hawks, including one that contained approximately 130 individuals, were observed foraging over several adjacent fields that were undergoing some form of cutting or harvesting. Many of these birds appeared to be making shallow aerial stoops, apparently chasing and capturing flying insects.

After fields were cut, or in the case of some fields that were recently irrigated, radio-tagged hawks were often observed foraging from the ground. These birds would wait for a small rodent or insect to pass by,

Table 1.   Home range information from radio-tagged Swainson's hawks in Yolo County, California, 1992.

HAWK SEX	CAPTURE DATE[a]	TOTAL HOURS TRACKED	TOTAL OBSERVA- TION POINTS	TOTAL FORAGING POINTS	TOTAL BIOLOGI- CALLY INDEPEN- DENT POINTS[b]	HOME RANGE (HA)[c]		
						95% MCP[d]	50% MCP	50% AK[e]
M	2 June	132	445	277	122	5339.0	21.0	32.7
M	10 July	120	380	268	80	2432.2	223.9	25.9
F	21 June	120	347	216	73	723.6	12.0	52.2
M	4 June	180	453	258	91	7658.8	88.9	82.2
Mean		138	406	255	92	4038.4	86.5	48.2

[a] Tracking ended 31 August.

[b] Total number of foraging points collected at a time interval (0.5 hr) sufficient to allow a radio-tagged Swainson's hawk to cross its home range.

[c] Based on biologically independent observation data.

[d] MCP = minimum convex polygon.

[e] AK = adaptive kernal.

and would then quickly pounce upon the particular prey item. Usually, the prey would be consumed on the ground where it was caught, especially if it was an insect (no attempt was made to identify prey items to taxonomic species). Fields containing 15–20 Swainson's hawks foraging from the ground were observed on two occasions in July and on three occasions in August.

DISCUSSION

Foraging ranges and total home range area of raptors are known to be influenced by prey abundance and prey accessibility (usually a function of vegetation cover and density), nest location, the total amount of available suitable foraging habitat within the home range, and type of vegetation (Wakeley 1978, Baker and Brooks 1981, Bechard 1982, Schmutz 1987, Estep 1989, Woodbridge 1991). Bechard (1982) reported a strong correlation between home range size of Swainson's hawks and the amount of suitable foraging habitat that was available. Preston (1990) found that red-tailed hawks (*Buteo jamaicensis*) and northern harriers (*Circus cyaneus*) responded to changes in prey abundance and cover density; patches of vegetation containing high prey populations but with dense vegetative cover were used by both species less frequently than predicted. In agricultural areas, the abundance and accessibility of prey such as small rodents and insects may change in response to growth, maturity, and harvest of certain crops. In the Sacramento Valley where

agriculture is the dominant land use, Estep (1989) found that as crops matured and vegetative cover increased, Swainson's hawks enlarged their foraging ranges in order to find more accessible prey; as crops and fields nearer the nest area were cut or harvested, the foraging range was reduced, sometimes even to a single field. Although no statistical analysis was conducted in this study to determine the correlation of home-range size with agricultural activities (crop cutting or harvesting), I suspect that foraging ranges of the radio-tagged Swainson's hawks increased in size as preferred crop types matured and prey become less accessible, and decreased during periods of harvesting and mowing when prey suddenly become more available.

In the Sacramento Valley, where changing agricultural markets and the juxtaposition of agriculture areas with urban development has resulted in a wide variety of agricultural cover types dispersed over very large areas, Swainson's hawk home ranges tend to be somewhat large. Estep (1989) reported a mean home range of 2760.4 ha for Swainson's hawks in the Central Valley, which compares to the large home ranges found in this study (despite the relatively small sample size in this study). However, in areas where the land use includes a predominance of cover types with a continually available prey base and abundant prey populations, Swainson's hawks may require substantially smaller home ranges in which to breed. Woodbridge (1991) found Swainson's hawks in northeastern California that nested

in areas surrounded by cover types that were high in prey density and prey accessibility and low in vegetative cover were associated with very small, circular home ranges (mean equal to 405.0 ha).

Grain crops, ruderal/fallow fields, row crops, tomatoes, and safflower were the dominant cover types in the study area. Estep (1989) found that crop patterns in the Central Valley that included a predominance of cover types with less overall vegetative cover and greater prey availability (i.e., alfalfa, fallow fields, dryland pasture) were preferred by Swainson's hawks and ranked highest in foraging use; grain crops and late-harvested row crops that had relatively small prey populations, and that were high in vegetative cover were less suitable as foraging habitat. The predominance of grain crops and row crops in my study area, combined with the large distances Swainson's hawks had to travel from nest sites to reach more compatible cover types, may explain the relatively large home ranges exhibited by the Swainson's hawks in this study. The presence of urban and residential areas to the north and east likely account for the somewhat linear nature of the home ranges in this study.

ACKNOWLEDGMENTS

LITERATURE CITED

BAKER, J.A. AND R.J. BROOKS. 1981. Distribution patterns of raptors in relation to density of meadow voles. *Condor* 83:42–47.

BECHARD, M.J. 1982. Effect of vegetative cover on foraging site selection by Swainson's hawk. *Condor* 84. 153–159.

BERGER, D.D. AND H.C. MUELLER. 1959. The bal-chatri: a trap for the birds of prey. *Bird-Banding* 30: 18–26.

BLOOM, P.H. 1980. The status of the Swainson's hawk in California. Fed. Aid in Wildlife Restoration, Proj W-54-R-12, Nongame Wildl. Invest., Calif. Dept. Fish and Game, Sacramento, CA U.S.A.

COLLISTER, A. 1967. Simple noose trap. *West. Bird Bander* 42:4.

ESTEP, J.A. 1989. Biology, movements and habitat relationships of the Swainson's hawk in the Central Valley of California, 1986–87. Calif. Dept. Fish and Game, Nongame Bird and Mammal Sec. Rep., Sacramento, CA U.S.A.

GRINNELL, J. AND A.H. MILLER. 1944. The distribution of the birds of California. *Pac. Coast Avif.* No. 27.

HAMERSTROM, F. 1963. The use of great horned owls in catching marsh hawks. Proc. Internat. Ornithol. Congr. 13:866–869.

LAIR, H. 1987. Estimating the location of the focal center in red squirrel home ranges. *Ecology* 68:1092–1101

PRESTON, C.R. 1990. Distribution of raptor foraging in relation to prey biomass and habitat structure. *Condor* 92:107–112.

SCHMUTZ, J.K. 1987. The effect of agriculture on ferruginous and Swainson's hawks. *J. Range Manage* 40(5):438–440.

WAKELEY, J.S. 1978. Factors affecting the use of hunting sites by ferruginous hawks. *Condor* 80:316–326.

WOODBRIDGE, B. 1991. Habitat selection by nesting Swainson's hawks: a hierarchial approach. M.S. thesis, Humboldt State Univ., Arcata, CA U.S.A.

WORTON, B.J. 1987. A review of models of home range for animal movement. *Ecol. Model.* 38:277–298.

DECLINING REPRODUCTION AMONG SWAINSON'S HAWKS IN PRAIRIE CANADA

C. Stuart Houston
863 University Drive, Saskatoon, SK, S7N 0J8, Canada

Josef K. Schmutz
Department of Biology, 102 Science Place, University of Saskatchewan, Saskatoon, SK, S7N 5E2 Canada

Abstract.—Swainson's hawk (*Buteo swainsoni*) population densities were apparently healthy and reproduction was consistently high in Saskatchewan (2.09 young per successful nest), and in southern Alberta (2.03 young per successful nest) through 1987. Our analysis of 2719 successful nestings revealed that near Kindersley, Saskatchewan, six consecutive years of declining production began in 1988, the worst 6 yr in 25 yr of study. Declines in production were evident at Hanna, Alberta by 1991. In 1993, productivity was only 1.14 young/successful nest near Hanna and 1.27 young/successful nest near Kindersley. The decline in productivity was accompanied by a drastic decline in the number of the Swainson's hawk's main prey, Richardson's ground squirrel (*Spermophilus richardsonii*).

Key Words: *Buteo swainsoni*; *Canada*; *population dynamics*; *reproductive decline*; *Swainson's hawk*.

Reproducción declinante de *Buteo swainsoni* en la Pradera Canadiense

Resumen.—Las densidades poblacionales de *Buteo swainsoni* estaban aparentemente saludables y la reproducción era consistentemente alta en Saskatchewan (2.09 juveniles por nido exitoso) y al sur de Alberta (2.03 juveniles por nido exitoso) durante 1987. Nuestro análisis de 2719 nidos exitosos reveló que cerca de Kindersley, Saskatchewan, que en 1988 comenzó una declinación productiva de seis años consecutivos, los peores seis años en 25 de estudio. La declinación en la producción fue evidente en 1991 en Hanna, Alberta. En 1993, la productividad cerca de Hanna fue solamente 1.14 juveniles por nido exitoso y 1.27 juveniles por nido exitoso cerca de Kindersley. La declinación en la productividad fue acompañada por una drástica declinación en número de la principal presa de *B. swainsoni*, una ardilla de la especie *Spermophilus richardsonii*.

[Traducción de Ivan Lazo]

Swainson's hawks (*Buteo swainsoni*) exhibit a generalist strategy in habitat occupancy and food habits (Schmutz et al. 1980). In western Canada, this hawk chiefly occupies grassland and parkland habitat. Even where these habitats have been substantially modified by agricultural cultivation, the Swainson's hawk remains common (Schmutz 1989). The Richardson's ground squirrel (*Spermophilus richardsonii*) is the main prey of Swainson's hawks throughout Alberta (Schmutz et al. 1980) and Saskatchewan (Houston 1990); the two species have precisely coterminous ranges in Alberta (Wonders 1969).

Swainson's hawk populations were stable in western Canada for three decades, but in 1987, a significant temporary increase in the number of breeding Swainson's hawks occurred in southern Alberta (Schmutz 1989). In this analysis we report on a more recently observed decline in reproduction.

Materials and Methods

We studied reproduction and population size in Swainson's hawks by intensively searching for nests and recording their success. Houston's most intensive study area was the vicinity of Kindersley, Saskatchewan (51–52°N, 108–110°W). The area was enlarged in 1987 to include Mantario, farther west near the Alberta boundary. Schmutz's area was near Hanna, Alberta, 120 km west of the Saskatchewan study area. The size of the Hanna study area changed over the years (335–480 km²), and we have chosen to standardize the Hanna data on a per 100 km² basis. A complete count of nests and young was made in 1975–77 and 1983–84 (Schmutz and Hungle 1989).

In Saskatchewan, no nests were approached closely during incubation because such disturbance can cause high levels of nest desertion (Houston 1974). Hence, an unknown number of nests had failed prior to the first visit in June or early July. Most often, banding occurred at a second visit, in late July. In Alberta, Swainson's nests were visited for the first time each year in early June. Nest occupancy was recorded without climbing to the nest
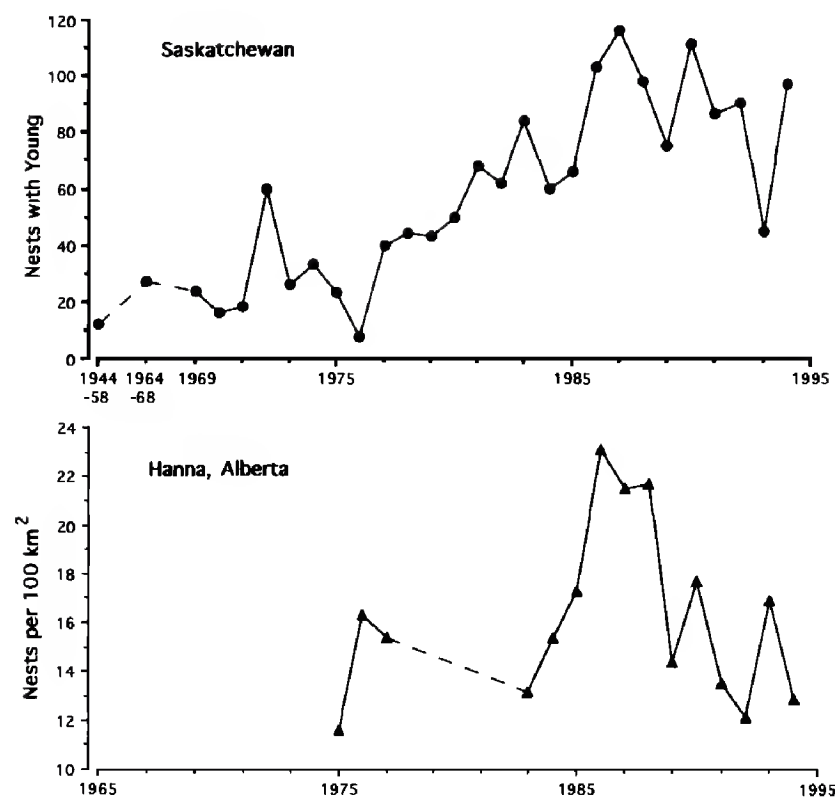
Figure 1.   Changes in numbers of Swainson's hawk nests in two study areas. On the Kindersley study area in Saskatchewan incremental increases in searching effort occurred in 1977, 1982, 1985 and 1993–94. The Hanna study area in Alberta (335 or 480 km²) was seached entirely and failed nests were included. The total number of successful nests was 1587 in Saskatchewan and 1131 in Alberta.
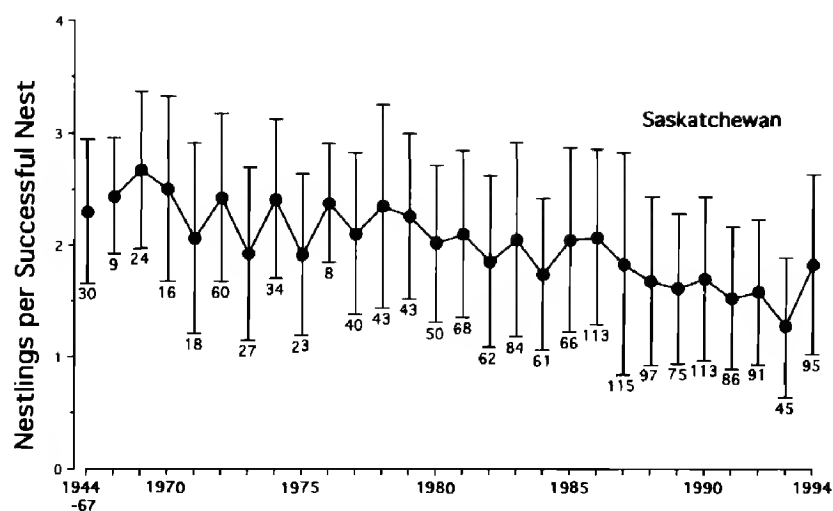

Figure 2.   The mean number of nestling Swainson's hawks per successful nest at the time of banding in Saskatchewan. Vertical bars are the standard deviation.

except in a few instances when the species of hawk could not be determined without causing the incubating bird to flush. All trees or shrubs within the study area boundary were examined for occupied nests. This method accounted for all or nearly all nesting attempts because even if deserted, nests were carefully inspected after climbing the tree or shrub if there was any indication of occupancy. Minimum evidence required for a breeding attempt was a completed and well-built nest with flattened lining. When no hawks defended such an abandoned nest, species of the occupant was ascertained from the type of nest material used (Schmutz et al. 1980).

RESULTS AND DISCUSSION

Nesting Densities. The number of nests found in Saskatchewan increased with greater search effort in the early years. Additional effort was expended when the drop in nesting pairs was evident again in 1993 and 1994 (Fig. 1).

In Alberta, nesting densities also changed. During three high-prey years (1986–88) densities averaged 22.1 nests/100 km² compared to 14.7 during 12 normal prey years.

Reproductive Success. Reproductive success is our strongest measure of the performance of Swainson's hawks for both populations. We visited both

populations for banding in mid-July to early August. Houston banded a total of 3047 Swainson's hawks (1 adult and 3046 nestlings) and Schmutz a total of 2585 (522 adults and 2063 nestlings).

In Saskatchewan, the number of young appeared relatively stable until 1987, with an average of 2.09 young per successful nest (Fig. 2). Beginning in 1988, the Swainson's hawk population showed a decline in productivity. Through 1993, the six consecutive worst years of productivity were recorded, averaging 1.60 young per successful nest, and significantly less than before the decline ($t = 5.73, 22$ df, $P = <0.0001$; Table 1). In 1993, productivity dropped to 1.27 young per successful nest; most pairs failed to raise young and even those that were successful at Kindersley, with three exceptions, raised only a single young per nest. At seven of 45 successful nests that year no adult appeared during 20-min banding visits, presumably because they were foraging at a great distance from the nest due to food shortage. In years of high prey numbers one or both parents were usually present close to the nest. An unprecedented number of failed nesting attempts (71 of 116) was encountered in 1993 (Table 1).

The decline was noticed first at the eastern part of the Saskatchewan study area near Kindersley in 1988 and became apparent 2 yr later at Mantario, Saskatchewan, and 1 yr later at Hanna, Alberta. In each region the decline was correlated with a visible diminution in the numbers of the chief prey, Richardson's ground squirrel, a decline that appeared to spread from east to west.

In 1994, a resurgence occurred at Kindersley to slightly below normal productivity per successful nest

Table 1. Swainson's hawks banded in Saskatchewan.

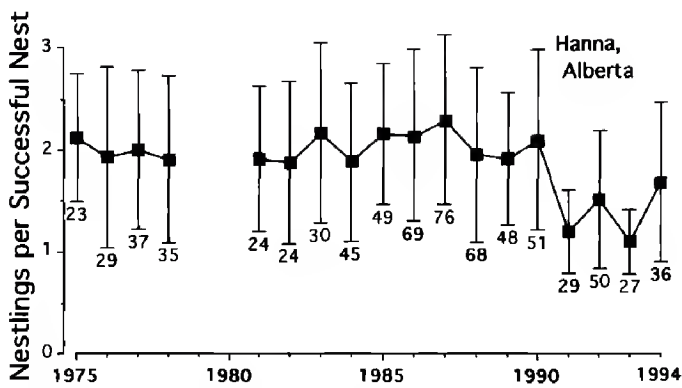| YEAR	N NESTS OB- SERVED	MINI- MUM FAIL- URE RATE	N YOUNG PER SUCCESSFUL NEST				MEAN N YOUNG PER SUC- CESS- FUL NEST
			1	2	3	4	
1944–1972	—	—	20	61	68	8	2.41
1973	50	46.0	9	11	7	0	1.93
1974	43	20.9	2	19	10	3	2.41
1975	42	45.2	7	11	5	0	1.91
1976	13	38.5	1	3	4	0	2.38
1977	56	28.6	9	18	13	0	2.10
1978	52	17.3	9	14	16	4	2.35
1979	53	18.9	8	16	19	0	2.26
1980	70	28.6	12	25	13	0	2.02
1981	82	17.1	15	32	20	1	2.10
1982	80	22.5	22	28	11	1	1.85
1983	109	22.9	26	32	22	4	2.05
1984	86	29.1	24	29	8	0	1.74
1985	86	23.3	20	24	21	1	2.05
1986	122	14.8	26	48	27	3	2.07
1987	143	19.6	61	19	28	7	1.83
1988	154	37.0	47	35	14	1	1.68
1989	132	43.2	37	30	8	0	1.61
1990	155	27.1	52	44	16	1	1.70
1991	124	30.6	47	32	7	0	1.53
1992	144	36.8	45	38	8	0	1.59
1993	116	61.2	37	4	4	0	1.27
1994	119	20.2	38	37	18	2	1.83
Total	2031	29.6	574	610	367	36	1.91

Figure 3. The mean number of nestling Swainson's hawks per successful nest at the time of banding in Alberta. Vertical bars are the standard deviation.

and above-average success of nesting attempts; this resurgence was not evident at Mantario where six nests fledged only nine young and 11 of 17 nesting attempts failed.

Over the entire Saskatchewan study area, most of the young were produced in nests with two or three young, and only 19% (574 of 3039 hawks) were produced in nests with one young (Table 1). Years when most nests produce only a single young may have serious consequences in regard to annual population replacement.

In contrast to the steady, 6-yr decline in Swainson's hawk reproduction in Saskatchewan, the decline in Alberta took a slightly different pattern. The yearly number of young per successful nest did not vary significantly through 1990 ($r_s = 0.048$, $P = 0.96$, $N = 14$ yr) with an average of 2.03 young per

successful nest. Thereafter, in 1991–94, the average was 1.43 young, declining significantly with the year ($r_s = -0.51$, $P = 0.03$, $N = 18$ yr), and being reflected both in the number of young per successful nest (Fig. 3) and in the total number of young fledged on the study area.

The decline in Swainson's hawk reproduction and breeding densities was evident in other studies in Saskatchewan and Alberta. In 1993, Jones (1993) checked 75 previously occupied Swainson's hawk nest sites in southern Alberta, and found only 10 young in six nests.

For both the Hanna and Kindersley study areas, the data are consistent with the interpretation that the recent decline in reproduction is due to an unexplained and substantial decline in ground squirrels Because declines among Swainson's hawks were widespread, factors operating on the 23 000 km migration route or on the wintering grounds in Argentina (Houston 1990) could also have influenced reproduction. Rappole and McDonald (1994) posed 14 criteria to help determine whether declining species are suffering mainly on their breeding grounds or on their wintering grounds. In the case of the Swainson's hawk, six of the Rappole-McDonald criteria (marginal breeding habitats, declines in optimal and usual breeding habitats, numbers varying with prey cycles, competition and replacement, and decrease in short-migrant grassland species) suggest that the major problem is on the breeding grounds. Eight other criteria they pose, four of which relate to wintering grounds, require further study.

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LITERATURE CITED

HOUSTON, C.S. 1974. Mortality in ringing: a personal viewpoint. *Ring* 80:157–161.

———. 1990. Saskatchewan Swainson's hawks. *Am. Birds* 44:215–220.

JONES, E.T. 1993. Summer '93: a catastrophic year for ferruginous and Swainson's hawk. *Alberta Nat.* 23(4): 14.

RAPPOLE, J.H. AND M.V. McDONALD. 1994. Cause and effect in population declines of migratory birds. *Auk* 111:652–660.

SCHMUTZ, J.K. 1989. Hawk occupancy of disturbed grasslands in relation to models of habitat selection. *Condor* 91:362–371.

——— AND D.J. HUNGLE. 1989. Populations of ferruginous and Swainson's hawks fluctuate in synchrony with ground squirrels. *Can. J. Zool.* 67:2596–2601.

———, S.M. SCHMUTZ AND D.A. BOAG. 1980. Coexistence among three species of prairie hawks (*Buteo* spp.) in the prairie-parkland ecotone of southeastern Alberta. *Can. J. Zool.* 58:1075–1089.

WONDERS, W.C. 1969. Atlas of Alberta. Univ. Alberta Press, Edmonton, AB, Canada.

Short Communications

An Investigation of the Swainson's Hawk in Argentina

Brian Woodbridge

USDA Forest Service, Klamath National Forest, 1312 Fairlane Road, Yreka, CA 96097 U.S.A.

Karen K. Finley

31338 S.W. Bellfountain Road, Corvallis, OR 97333 U.S.A.

S. Trent Seager

1016 15th Street, Bellingham, WA 98225 U.S.A.

Information on the distribution and ecology of Swainson's hawks (*Buteo swainsoni*) during the nonbreeding season is limited. Large numbers have been counted annually during migration in Mexico (Thiollay 1980, Tilly 1992) and Panama (Smith 1985), but records in South America are limited to scattered band recoveries and anecdotal field observations. Most sightings and band recoveries of Swainson's hawks during the nonbreeding period have come from the Argentinean provinces of Buenos Aires, La Pampa, Cordoba, and Santa Fe (CIPA Sección Argentina 1987, White et al. 1989, Houston 1990). However, the low numbers reported in Argentina have led Smith (1985) to predict a wintering population elsewhere in South America.

Here we report the results of a pilot study conducted between October 1994 and February 1995. Our objectives included identifying migratory routes of Swainson's hawks from our study area in Butte Valley, northern California, locating important austral destinations, and studying habitat relationships of Swainson's hawks during the nonbreeding period.

Methods

In July 1994 we captured two adult female Swainson's hawks at their nests in the Butte Valley National Grasslands, Klamath National Forest, California and fitted them with 28-g satellite radiotransmitters (Microwave Telemetry Inc., Columbia, Maryland). Transmissions were received by NOAA weather satellites and relayed to the ARGOS Inc. data processing center, Maryland.

Between 23 January and 4 February 1995, we visited the area in Argentina where the majority of transmissions occurred. We established a 6400-km² study area encompassing several satellite locations located near the northern border of La Pampa Province, roughly between the towns of Colonel Hilario Lagos and General Pico. The landscape within the study area was mixed agriculture of corn, sunflowers, soybeans, hay, and pasture. Pasture vegetation (mixed clover and grasses) was intensively managed by rotation of livestock through a system of small paddocks. The proportions of pasture and cultivated crops in the study area were approximately equal. Marginal lands, uncultivated roadsides, native pastures and wetlands were also important parts of the landscape.

We conducted surveys along roads at 5-km intervals, recording location and behavior of Swainson's hawk flocks, roost sites, and habitat. Surveys were conducted from 0530–1200, and 1600–2000 H. We made ocular estimates of the size of foraging flocks and estimated the numbers of hawks departing roosts in early morning hours. In addition, we interviewed local farmers about current agricultural practices and historical and anticipated land use changes.

Results and Discussion

Migration. Hawk #1 began migration on 20 September, traveled south through California, and then into western Arizona (26 September) where its transmitter failed. She returned to her breeding territory in northern California in late April 1995.

Hawk #2 began migration in early October and followed the same route as Hawk #1, settling in the vicinity of Tempe and Phoenix, Arizona from 6 October to 12 October. After 15 October this hawk moved southeast to Tamaulipas on the Gulf Coast of Mexico (24 October), and rapidly though Central America (Santa Ana, El Salvador (30 October), and Lago de Nicaragua (2 November). Poor satellite coverage in the equatorial region caused inadequate location until the bird reached southwest Brazil (18 November to 24 November). Crossing into Argentina in late November, Hawk #2 moved south (27 November to 3 December), then remained in the northern portion of the province of La Pampa for nearly 6 wk (11 December to 28 January). The last transmission (28 January) was approximately 340 km north of that area, and possibly indicated initiation of northward migration. This female was observed near her breeding territory in June 1995.

Abundance, Behavior, and Habitat Use. Flocks observed at six night roosts ranged from 35–7000 individuals ($\bar{x}$ = 2300 individuals/roost). Roosts were groves of exotic *Eucalyptus* sp. trees (10–30 m tall) which surrounded many ranch houses or long windbreaks at the edges of fields. These stands ranged from 5–30 ha in size and were typically the only trees available over large areas.

Foraging groups ranged from 50–1000 individuals, with one large flock estimated at 4000. We estimated the total number of Swainson's hawks observed within the study area to be approximately 20 000 (±4000). Estimation of Swainson's hawk numbers within the study area was difficult due to high mobility of foraging flocks and unpredictable use of night roosts.

Flocks within our study area were dominated by light-phase adult hawks. During our study period we observed seven banded Swainson's hawks, and recovered three U.S. Fish and Wildlife Service bands from carcasses at a night roost. Two of these were banded as nestlings in northern Saskatchewan and Colorado, respectively. The third was banded as a breeding adult in our California study area. The other four banded Swainson's hawks were seen perched or flying. Two color-banded hawks were from California (black or yellow bands), and two had metal bands. Each of these four sightings was made in a different flock. The band recoveries suggest that the flocks consisted of individuals from different regions of the species' breeding range.

Flocks typically left the roosts in the early morning hours and frequently settled nearby on the ground or on fenceposts, where they foraged for grasshoppers (*Dichropulus* spp. and possibly others) in older pastures and recently cultivated soil. As air temperatures rose, smaller bands began foraging on the wing and moving across the landscape. Groups were also seen following tractors as they mowed or baled alfalfa. Most observations were of Swainson's hawks foraging in or above older, weedy pastures where grasshoppers were obviously abundant. Flocks were also observed capturing insects on the wing; at these times their habitat associations were less clear. Pellets collected beneath roost sites were composed entirely of orthopterans.

At one large roost containing approximately 4000 Swainson's hawks we saw numerous Swainson's hawk carcasses on the ground. We conducted a complete search along transects throughout the roost and recorded over 700 dead Swainson's hawks. According to the landowner the hawks died after consuming grasshoppers that had been sprayed with an unknown pesticide in a nearby pasture about one month earlier (21 December 1994). He said the birds had flown back to the roost and were seen dying there for several days immediately after the spray event. This description of the birds' symptoms suggested organophosphorus or carbamate insecticide poisoning. Evidence of fatal poisoning was not observed during searches of other known roosts.

Satellite telemetry promises to be a valuable tool for identifying the migratory route and austral locations of Swainson's hawks breeding in North America. Locating these austral sites is a critical first step in describing the nonbreeding season ecology of migrant raptors and identifying potential threats to populations (Senner and Fuller 1989). Based on previous band recoveries and our obser-

vations, we suspect that the northern La Pampa area supports an important concentration of Swainson's hawks during the nonbreeding season. However, deployment of additional transmitters on individuals from separate populations will be necessary to gain a more complete picture of the austral distribution and movements of this species.

Our observation of direct mortality due to pesticide poisoning signals the potential vulnerability of wintering Swainson's hawks, which forage on grasshoppers targeted for chemical control. Small, localized breeding populations may be particularly vulnerable if they remain together during the nonbreeding season in austral locations (Bloom 1980). Although mortality on the scale we observed may be an isolated event, based on discussions with biologists and ranchers in Argentina we suspect that pesticide contamination is not unusual. Our initial findings lead us to believe that it is likely that the transformation of Argentinean agriculture from a system of range-based livestock production to one of intensive agricultural cultivation will have negative impacts on Swainson's hawks and other insectivorous birds. Development and implementation of effective conservation strategies for Swainson's hawks and other migratory avian species will be dependent on international collaboration. This will require documentation of changes in land use and agricultural practices, as well as assessment of hawk populations in both breeding and nonbreeding regions.

RESUMEN.—Usamos la telemetría satélite para estudiar la ruta migratoria y la destinación austral principal de dos aguiluchos langosteros (*Buteo swainsoni*) del norte de California, U.S.A. Los aguiluchos migraban a través el valle central de California, al este a través Arizona, la costa este de Mexico, a través El Salvador y Nicarágua en América Central, y hacia el este de los Andes a Argentina. Una aguilucha se quedó en el norte de la provincia de La Pampa, Argentina por seis semanas. En La Pampa, se encontraron grandes cantidades de los aguiluchos langosteros en pastizal y habitat agrícola. Se observaron 35–7000 individuos en dormideros de *Eucalyptus* sp., y bandadas de foraje de 50–1000 individuos. Los aguiluchos se alimentaron principalmente de *Dichropulus* spp. (Orthopterans) en habitat pastizal. Observamos 15 000–20 000 ejemplares dentro una área de 6400 km². En un dormidero grande, recordamos mas de 700 aguiluchos langosteros muerte. Ellos se murieron después de la applicación aérea de pesticidas.

[Traducción de Karen Finley]

LITERATURE CITED

BLOOM, P.H. 1980. The status of the Swainson's hawk in California, 1979. Final Rept. II-8.0, Bur. Land Manage. and Fed. Aid in Wildlife Restoration, Proj. W-54-R-12, California. Dept. Fish and Game, Sacramento, CA U.S.A.

CIPA SECCIÓN ARGENTINA. 1987. La presencia actual del aguiluchoangostero en la Argentina. *Nuestras Aves* 13:13–16. Assoc. Ornit. del Plata, Buenos Aires.

HOUSTON, C.S. 1990. Saskatchewan Swainson's hawks. *Am. Birds* 44:215–220.

SENNER, E.S. AND M.R. FULLER. 1989. Status and conservation of North American raptors migrating to the neotropics. Pages 53–57 *in* B.-U. Meyburg and R.D. Chancellor [EDS.], Raptors in the modern world. World Working Group on Birds of Prey and Owls, Berlin, Germany.

SMITH, N.G. 1985. Some uncertain aspects of migration by Swainson's hawks (*Buteo swainsoni*) and turkey vultures (*Cathartes aura*). Proc. North American Hawk Migration Conf. No. 4., Rochester, NY U.S.A.

THIOLLAY, J.M. 1980. Spring hawk migration in eastern Mexico. *Raptor Res.* 14:13–20.

TILLY, F.C. 1992. Hawk-watching's little known sites *Birding* 1992:10–16.

WHITE, C.M., D.A. BOYCE AND R. STRANEX. 1989. Observations on migrant *Buteo swainsoni* in Argentina, 1984. Pages 79–87 *in* B.-U. Meyburg and R.D. Chancellor [EDS.], Raptors in the modern world. World Working Group on Birds of Prey and Owls, Berlin, Germany.

RECOVERY OF A RESIDENT POPULATION OF OSPREY ON CORSICA

JEAN-CLAUDE THIBAULT
Parc Naturel Régional de la Corse, B.P. 417, F-20184 Ajaccio, Corsica

VINCENT BRETAGNOLLE
Centre d'Études Biologiques de Chizé, Centre National de la Recherche Scientifique, F-79360 Beauvoir-sur-Niort, France

JEAN-MARIE DOMINICI
Parc Naturel Régional de la Corse, B.P. 417, F-20184 Ajaccio, Corsica

Two factors have been shown to be major causes of the decline of osprey (*Pandion haliaetus*) in Europe between 1940 and 1970: (1) persecution during breeding and migration (Bijleveld 1974, Saurola 1985), and (2) extensive use of pesticides, especially organochlorines (Ratcliffe 1967, Newton 1979, Odsjö 1982). But since the 1970s, osprey numbers have increased rapidly in Europe. This has been especially well documented for the migrant northern populations (Bird et al. 1983, Dennis 1987, Poole 1989). Conversely, the literature for resident populations is scarce. Mediterranean population increases apparently were consistently lower, with stable populations reported in some areas (Thibault et al. in press.). The reasons for this difference are unknown, but patterns of recolonization and recovery might be different between resident and migrating populations (e.g., adult and juvenile survival rates, or both, may differ).

The island of Corsica has a resident population of ospreys known to occupy nearly all of its rocky coasts. The historic distribution is shown in Fig. 1a. Additionally, on the east coast which is flat and sandy at least two pairs bred in gorges several kilometers inland, and two others on off-shore rocky islets (Terrasse and Terrasse 1977, Thibault and Patrimonio 1990). The number of breeding pairs between the end of the 19th century and the 1960s is unknown because no counts were performed, but it was estimated at 40–100 pairs (Thibault and Patrimonio 1990) Here we report patterns of abundance and geographic distribution of the osprey in its population increase on Corsica from 1977–94.

STUDY AREA AND METHODS

The total osprey population on Corsica in the western Mediterranean Ocean (42°N, 9°E) has been monitored annually from 1977–94. The breeding season of this resident population is spread over 6 mo, from February to July (Thibault and Patrimonio 1991). Osprey in the Mediterranean have semi-colonial habits, breeding within 80–500 m of each other (Thibault et al. in press). Osprey in Corsica nest only on pinnacles along the rocky seacoast (Thibault and Bouvet 1983). This facilitated observing nests using telescopes (20–45×) from less than 300 m away, permitting a good view into nests. Eyries were checked at least once a month from March to August. We
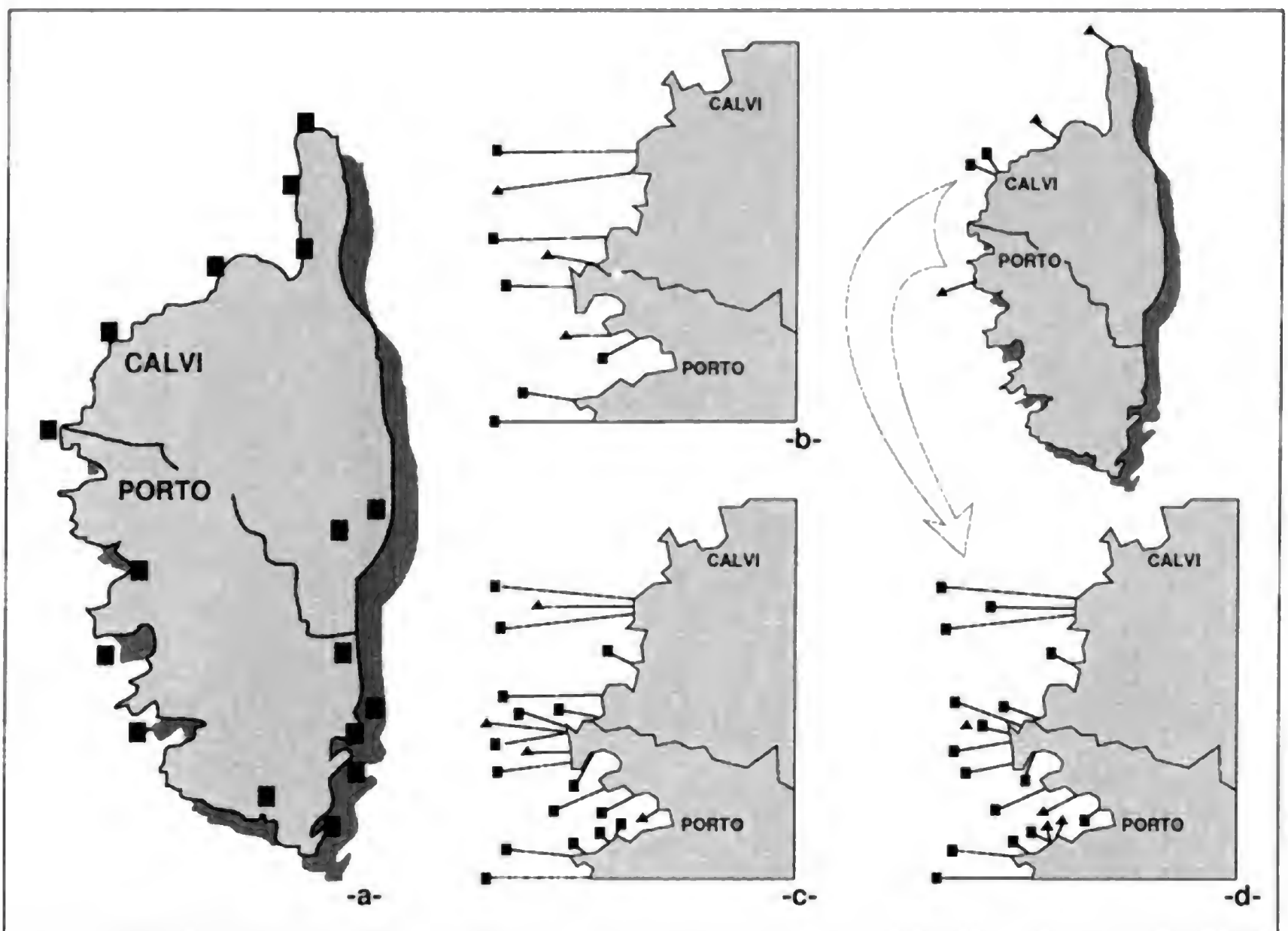
Figure 1. Distribution of the osprey on Corsica: (a) historic data from the end of the 19th century to the 1960s (squares indicate historic breeding sites [Thibault and Patrimonio 1990]), (b) distribution in 1977, (c) distribution in 1990, and (d) distribution in 1994 (squares indicate breeding pairs; triangles indicate nonbreeding pairs).

also checked sites listed in Thibault and Patrimonio (1990) that are unoccupied today, for which historic data and locations were obtained from literature or with the help of local residents. These sites were also checked regularly between 1977–94. All occupied nests were taken into account, but we distinguished between active nests (with at least one egg), and nests occupied by nonbreeding pairs (with no clutch). To calculate the population density, location of all occupied nests was plotted on 1:25 000 scale maps (Institut Géographique National, France). Distances between nests were then calculated with a curvimeter following the coastline.

RESULTS

Trends in the number of both active nests and nests occupied by nonbreeding osprey from 1977–94 are presented in Fig. 2. During this period, the number of breeding pairs increased steadily from 6–18 at the annual average growth rate of 6.7% ($r_{16} = 0.93$, $P < 0.001$).

Until 1990, the whole breeding population was confined to the region between the cities of Calvi and Porto. In 1977, six breeding pairs were spread over 90 km along the northwest coast (Fig. 1b), with a mean distance between nests of 13.9 km (SD = 6.3, range = 7–23 km, $N = 6$) and 7.5 km (SD = 2.9, range = 5–12.2 km, $N = 9$) for active and occupied nests, respectively. By 1990, the number of breeding pairs had increased to 16, but the birds were distributed within exactly the same area as in 1977 (Fig. 1c). As a result, the mean distance between nests decreased to 3.9 km (SD = 1.99, range = 2–9 km, $N = 16$) and 3.24 km (SD = 2.35, range = 1–9 km, $N = 20$) for active and occupied nests, respectively. From 1990–94, osprey distribution in Corsica increased, while the number of breeding pairs was only slightly higher. Considering only the original area, the mean distance between nests since 1990 has remained constant (3.9 km, SD = 1.99, $N = 16$ in 1990; and 3.4 km, SD = 2.5, $N = 16$ in 1994), i.e., no new pairs became established there after 1990. This suggests that the initial area was saturated by 1990. Thus, the increase in number from 1990–94 involved
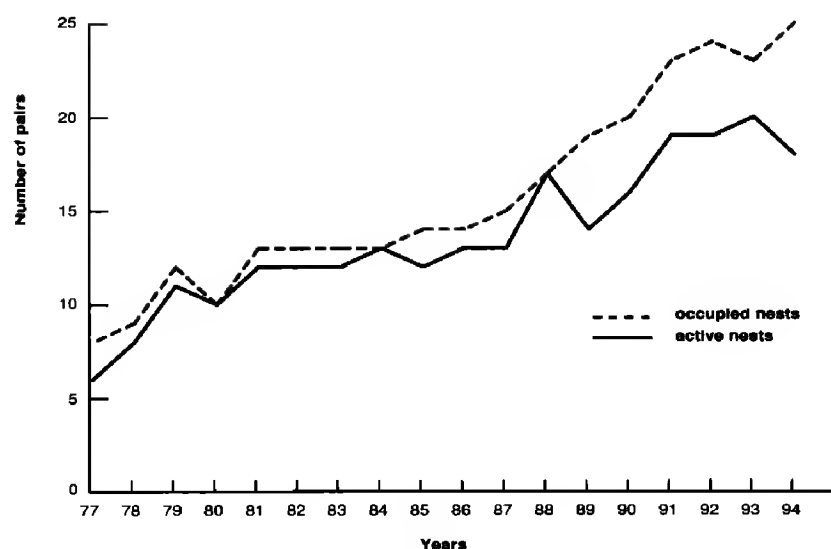
Figure 2. Trends in osprey numbers in Corsica 1977–94. Active nests were those that produced at least one egg, and occupied nests were those attended by osprey that did not lay eggs.

several pairs that recolonized former breeding sites—sites that had not been occupied for at least 20–30 yr. In 1994, a total of five pairs (two breeding and three nonbreeding) were in this situation (Fig. 1d).

DISCUSSION

The decrease of osprey on Corsica appears to have been most severe among isolated pairs—those that were distributed in areas where favorable habitats were limited and where colonies of birds did not exist. Conversely, on the northwest coast of the island, human pressure was very low and favorable habitats enabled the birds to breed at high densities. In the latter area, osprey were able to maintain a minimum number of pairs, thus preventing total disappearance from the island. Recovery of osprey populations to historic numbers is unlikely because several historic breeding sites, especially in the southeastern part of the island, are now surrounded by housing developments. Two facts in the pattern of recovery in Corsica are strikingly different from what was observed in northern European populations. First, the average annual population increase was lower in Corsica (7%, 1977–94) than in Scotland (15%, 1962–86; Dennis 1987). Second, the population remained in exactly the same area for 15 yr while numbers increased threefold before shifting to new sites. We suggest that annual population increase in Corsica is lower because new recruits were mainly local recruits. Conversely, in Scotland a Scandinavian origin for some at least of the recruits is well established (Dennis 1987). Although we cannot ascertain that the increase was entirely attributable to local recruits rather than through immigration to Corsica, banding nestlings with color bands since 1980, and field identification of adults using individual variation in the coloration of head feathers (Bretagnolle et al. 1994), strongly suggest that the new birds are mainly local recruits. The second difference may result from a combination of (1) the semi-colonial habits of the osprey (Bretagnolle and Thibault 1993), which, like other colonial birds, tends to use sites that are already being used by conspecifics (Buckley and Buckley 1980, Burger and Gochfeld 1990), and (2) the insularity of Corsica. The osprey appears to be more colonial in Corsica than in Scotland or elsewhere in northern Europe, possibly as a consequence of breeding entirely in continuous coastal habitats on Corsica, rather than on lakes (i.e., discrete habitats) as in other parts of Europe. It is also possible that nonmigratory habits of ospreys in Corsica might have further reduced natal dispersal in the population.

As a result of these differences, the increasing population of Corsican ospreys occupied the same range for nearly 15 yr, before expanding its range to other sites on the island (though these were all occupied historically) when the initial area was saturated.

RESUMEN.—Hemos estudiado la reproducción del Aguila pescadora *Pandion haliaetus* en la isla de Corcega, Mediterraneo occidental, desde 1977 hasta 1994. La antigua distribución, desde el final del siglo XIX hasta 1960, basda sobre datos historicos, demuestra que ocupaba casi todas las costas rocosas. La población estaba estimada entre 40–100 parejas. En 1977, se redujo a 6 parejas repartidas sobre 90 km de la costa Norte-Oeste. En 1990, el número de parejas reproductoras era de 16, para une distribución en los mismos limites que en 1977. Desde 1990 hasta 1994, la región parecia saturada, puesto que varias parejas habian reconquistado antiguos lugares en el norte de la isla, inocupados desde 20–30 años. Las modalidades de crecimiento de efectivos, y su distribución son discutidos en función de las especifidades de esta población residente.

[Traducción de Helena Perez]

LITERATURE CITED

BIJLEVELD, M. 1974. Birds of prey in Europe. MacMillan Press, London, U.K.

BIRD, D.M., N.R. SEYMOUR AND J.M. GERRARD [EDS.]. 1983. Biology and management of bald eagles and ospreys. Harpell Press, Ste. Anne de Bellevue, Québec, Canada.

BRETAGNOLLE, V. AND J.-C. THIBAULT. 1993. Communicative behavior in breeding ospreys (*Pandion haliaetus*): description and relationship of signals to life history. *Auk* 110:736–751.

————, J.-C. THIBAULT AND J.-M. DOMINICI. 1994. Head patterns allow field identification of individual ospreys. *J. Wildl. Manage.* 58:175–178.

BUCKLEY, F.G. AND P.A. BUCKLEY. 1980. Habitat selection and marine birds. Pages 69–112 in J. Burger, B.L. Olla and H.E. Winn [EDS.], Behavior of marine animals. Plenum Press, New York, NY U.S.A.

BURGER, J. AND M. GOCHFELD. 1990. The black skim-

mer. Social dynamics of a colonial species. Columbia Univ. Press, New York, NY U.S.A.

DENNIS, R. 1987. Osprey recolonisation. *Royal Soc. Pres. Birds Conserv. Rev.* 1:88–90.

NEWTON, I. 1979. Population ecology of raptors. T. and A.D. Poyser, Berkhamsted, U.K.

ODSJÖ, T. 1982. Eggshell thickness and levels of DDT, PCB, and mercury in eggs of osprey and marsh harrier in relation to their breeding success and population status in Sweden. Ph.D. dissertation, Univ. Stockholm, Stockholm, Sweden.

POOLE, A.F. 1989. Ospreys. A natural and unnatural history. Cambridge Univ. Press, Cambridge, U.K.

RATCLIFFE, D.A. 1967. Decrease in eggshell weight in certain birds of prey. *Nature* 215:208–210.

SAUROLA, P. 1985. Persecution of raptors in Europe assessed by Finnish and Swedish ring recovery data. Pages 439–448 *in* I. Newton and R.D. Chancellor [EDS.], Conservation studies of raptors, Tech. Pub. 5. Internat. Council Bird Pres., Cambridge, U.K.

TERRASSE, J.-F. AND M. TERRASSE. 1977. Le Balbuzard pêcheur *Pandion haliaetus* (L.) en Méditerranée occidentale. Distribution, essai de recensement, reproduction, avenir. *Nos Oiseaux* 34:111–127.

THIBAULT, J.-C. AND F. BOUVET. 1983. Les caractéristiques du nid du Balbuzard pêcheur *Pandion haliaetus* en Corse. *Nos Oiseaux* 37:65–73.

——— AND O. PATRIMONIO. 1990. La conservation du Balbuzard pêcheur (*Pandion haliaetus*) en Corse. *Trav. Sc. Parc naturel rég. & Réserves nat. Corse* 27:63–83.

——— AND ———. 1991. Some aspects of breeding success of the osprey *Pandion haliaetus* in Corsica, West Mediterranean. *Bird Study* 38:98–102.

———, R. TRIAY, P. BEAUBRUN, D. BOUKHALFA, J.-M. DOMINICI AND A. TORRE. Osprey (*Pandion haliaetus*) in the Mediterranean: characteristics of a resident population with a patchy distribution. Soc. Esp. Orn.-BirdLife Int., Madrid, Spain. In press.

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A COMPARISON OF TWO METHODS FOR STUDYING THE DIET OF THE PEREGRINE FALCON

DANIEL ORO
Departament de Biologia Animal -Vertebrats-, Universitat de Barcelona, Avda. Diagonal, 645, 08028 Barcelona, Spain

JOSÉ L. TELLA[1]
Estación Biológica de Doñana, CSIC, Avda. María Luisa s/n, Pabellón del Perú, 41013 Sevilla, Spain

A frequent difficulty in the study of raptor diets is determining how valid the results are as the result of the sampling methodology. Stomach contents, pellets, prey remains, and direct observation are the main methods applied (Marti 1987). Many studies have used just one of these methods (e.g., Bustamante 1985, Nielsen and Cade 1990, Tella 1991). Others used a combination of some of them (e.g., Restani 1991, Mañosa and Cordero 1992, Underhill-Day 1993), but biases produced by the different methods have been tested only for few species (Collopy 1983, Simmons et al. 1991, Hunt et al. 1992, Mersmann et al. 1992, Real 1991, Mañosa 1994).

The aims of this paper are (1) to compare pellet contents with uneaten prey remains in determining the diet of the peregrine falcon (*Falco peregrinus*), and (2) to develop a

more accurate method to evaluate peregrines' diet by using both methods separately or in conjunction.

METHODS

The study was carried out on 7500 km^2 in the Ebro Valley, northeastern Spain (Tella 1991, 1993). Diet samples were collected from below cliffs used by 19 breeding pairs of peregrine falcons that remained in the area year-round. The collections were made between 1987 and 1993, on a regular basis throughout the year to avoid biases associated to seasonal variations in the diet (Mearns 1982, 1983). Collections were carried out by one or two people carefully searching for pellets and small remains for 45–120 min (Langvatn 1977). Each collection of prey remains and pellets from a pair on one date was considered to be a sample. Prey remains were identified using our comparison collection of bones and feathers and those from the Museum of Zoology of Barcelona. Mass of prey was estimated from the literature (Geroudet 1946–57, Cramp and Simmons 1977–83, Cramp 1985–93) and our own data from the study area.

Diet was determined separately from the number of prey items identified in pellets and from uneaten prey

Table 1. Number of prey (N_p) and species (N_s) identified by two methods and the combination of both methods (Total). Species or families with N_p < 10 were grouped.

	REMAINS		PELLETS		TOTAL	
	N_p	N_s	N_p	N_s	N_p	N_s
Anseriformes	11	3	0	0	11	3
Galliformes	12	1	0	0	12	1
Columbiformes	291	5	14	1	291	5
Pteroclidiformes	25	2	0	0	25	2
Strigiformes	9	2	2	1	11	2
Apodiformes	36	2	4	1	38	2
Coraciformes	26	2	2	2	26	2
Piciformes	17	1	0	0	17	1
Sturnidae	58	2	40	1	64	2
Corvidae	45	5	1	1	46	5
Turdidae	29	3	3	2	31	3
Unidentified passerines	149	31	62	11	181	32
Unidentified birds	15	5	1	1	15	6
Lagomorpha	24	2	1	1	25	2
Unidentified mammals	5	2	4	1	9	2
Unidentified reptiles	2	1	0	0	2	1
Arthropoda	0	0	16	3	16	1
Total	754	69	150	26	820	74

remains in each sample. Additionally, the two methods were combined by considering the minimum number of prey identified from each unit sample (e.g., the number of spotless starlings [Sturnus unicolor] where we identified two starlings by remains and one starling by pellets would be two).

Results obtained by the analysis of pellets and remains were contrasted in different ways. We used the Margalef index (IM; Magurran 1988) to calculate species richness. However, due to the high number of identified species (N = 81), we grouped prey by ordinal taxa (except in passerines where we separated the three families most often preyed upon and the rest) for statistical purposes. Overlap of the results was expressed through the Pianka index (Pianka 1973). An exponential distribution in base two was used to group the prey by mass categories. Differences between taxa or weight distributions of prey obtained by both methods were tested with chi-square tests on contingency tables, applying the Bonferroni correction to ensure an overall α < 0.05 when we separately compared weight intervals (Zar 1984).

RESULTS

We obtained 72 collections of prey remains and 81 pellets. Analysis showed low overlap between remains and pellet contents by taxa (Pianka's index = 0.61; Table 1). The species richness was greater in the prey remains (IM = 6.55) than in the pellets (IM = 4.42), although the lower species diversity in pellets may be due to the high number of small passerines not identified to the species level. The number of prey as well as the number of species identified in the remains (754 individuals, 69 species) was greater than that identified in the pellets (150 individuals,

26 species). The differences between these results and the totals obtained by means of the combined method (820 individuals, 71 species) were statistically significant (χ^2 = 899.21, df = 1, P < 0.0001 for remain analysis; χ^2 = 51.85, df = 1, P < 0.0001 for pellet analysis).

Results grouped by taxa (Table 1) clearly differed between remain and pellet analyses (χ^2 = 212.34, df = 16, P < 0.0001). Prey mass distribution also showed strong differences between the two methods (χ^2 = 172.7, df = 7, P < 0.0001; Fig. 1). Small prey were seldom detected in the remains. Large prey were found more often in the remains than in the pellets. Thus, pellet analysis would indicate that this peregrine population mainly consumed small- to medium-sized prey (17–128 g), while analysis of remains of the same diet would indicate a preference for the larger prey (257–512 g; Fig. 1).

DISCUSSION

Direct observations of peregrines (Dekker 1980, Bird and Aubry 1982, Thiollay 1982, Ward and Laybourne 1985) may be the best method to determine diet, but it requires a great deal of time and is often inpractical (Marti 1987). The collection of prey remains and pellets of peregrine are more practical ways to describe their diet, and they have been widely used by several authors (see review in Porter et al. 1987). Nevertheless, Mearns (1982, 1983) suggested that there were differences between the results of analyses of remains and pellets. Our results confirm these differences, and showed that the diet of the same peregrine population can offer contrasting results depending on the method used.

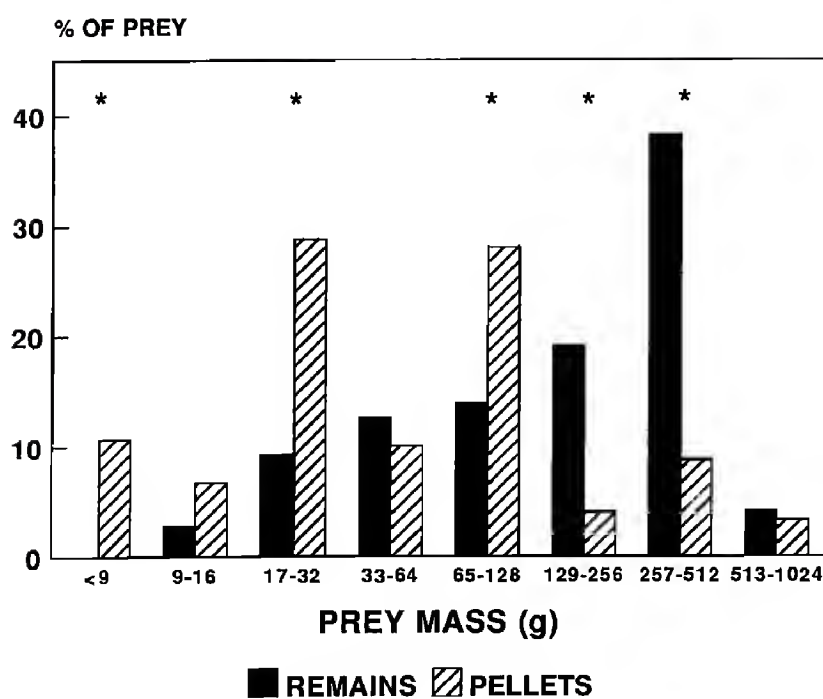The absence of direct observations at nests made it difficult to evaluate which of our methods was best. None-

% OF PREY

Figure 1. Mass distribution of prey identified by means of prey remains or pellet analysis. Differences were tested by χ^2 tests applying Bonferroni correction to ensure $\alpha < 0.05$. Significant differences ($P < 0.0001$) are indicated with an *.

theless, due to the very different results derived from the analysis of remains and pellets, we recommend their combined use as suggested for other birds of prey (Simmons et al. 1991, Mersmann et al. 1992, Mañosa 1994). However, small prey could still be underestimated due to the low number and low detectability of pellets, particularly under unfavorable weather conditions. In addition, the removal of large prey remains by scavengers (e.g., red fox [*Vulpes vulpes*], which often visits breeding sites of Egyptian vulture [*Neophron percnopterus*] and peregrine falcons, Tella and Torre 1990), may also reduce their detection. These biases could be avoided to a great extent by increasing the frequency of collections (e.g., Reynolds and Meslow 1984).

RESUMEN.—Hemos estudiado la dieta del halcón peregrino (*Falco peregrinus*) en el noreste de España mediante la recolección de restos de presas y el análisis de egagrópilas. Ambos métodos difieren marcadamente en sus resultados: las presas pequeñas aparecen en menor proporción entre los restos, mientras que las grandes son subestimadas en las egagrópilas. Las egagrópilas desaparecen probablemente con mayor rapidez que los restos. Recomendamos por ello el uso combinado de ambos métodos y la realización de frecuentes recolecciones, con el fin de reducir sesgos en los resultados.

[Traducción autores]

LITERATURE CITED

BIRD, D.M. AND Y. AUBRY. 1982. Reproductive and hunting behaviour in peregrine falcons, *Falco peregrinus*, in Southern Québec. *Can. Field-Nat.* 96:167–171.

BUSTAMANTE, J. 1985. Alimentación del Ratonero Común (*Buteo buteo*) en el norte de España. *Doñana Act. Vert.* 12:51–62.

COLLOPY, M.W. 1983. A comparison of direct observations and collections of prey remains in determining the diet of golden eagles. *J. Wildl. Manage.* 47:360–368.

CRAMP, S. [ED.]. 1985–93. The birds of the western Palearctic. Vols. 4–7. Oxford Univ. Press, Oxford, U.K.

——— AND K.E.L. SIMMONS. 1977–83. The birds of the western Palearctic. Vols. 1–3. Oxford Univ. Press, Oxford, U.K.

DEKKER, D. 1980. Hunting succes rates, foraging habits, and prey selection of peregrine falcons migrating through central Alberta. *Can. Field-Nat.* 94:371–382.

GEROUDET, P. 1946–57. La vie des oiseaux. Vols. 1–6. Collection de Poche. Les Beautes de la Nature. Delachaux and Niestle S.A., Paris, France.

HUNT, W.G., J.M. JENKINS, R.E. JACKMAN, C.G. THELANDER AND A.T. GERSTELL. 1992. Foraging ecology of bald eagles on a regulated river. *J. Raptor Res.* 26: 243–256.

LANGVATN, R. 1977. Characteristics and relative occurrence of remnants of prey found at nesting places of gyrfalcon *Falco rusticolus*. *Ornis Scand.* 8:113–125.

MAGURRAN, A.E. 1988. Ecological diversity and its measurement. Croom Helm Eds., London, U.K.

MAÑOSA, S. 1994. Goshawk diet in a mediterranean area of northeastern Spain. *J. Raptor Res.* 28:84–92.

——— AND P.J. CORDERO. 1992. Seasonal and sexual variation in the diet of the common buzzard in northeastern Spain. *J. Raptor Res.* 26:235–238.

MARTI, C.D. 1987. Raptor food habit studies. Pages 67–80 *in* B.A. Giron Pendleton, B.A. Millsap, K. Cline and D.M. Bird [EDS.], Raptor management techniques manual. Natl. Wildl. Fed. Washington, DC U.S.A.

MEARNS, R. 1982. Winter occupation of breeding territories and winter diet of peregrines in south Scotland. *Ornis Scand.* 13:79–83.

———. 1983. The diet of the peregrine *Falco peregrinus* in south Scotland during the breeding season. *Bird Study* 30:81–90.

MERSMANN, T.J., D.A. BUEHLER, J.D. FRASER AND J.K.D. SEEGAR. 1992. Assessing bias in studies of bald eagle food habits. *J. Wildl. Manage.* 56:73–78.

NIELSEN, O.K. AND T.J. CADE. 1990. Seasonal changes in food habits of gyrfalcons in ne-Iceland. *Ornis Scand.* 21:202–211.

PIANKA, E.R. 1973. The structure of lizard communities. *Ann. Rev. Ecol. Syst.* 4:53–74.

PORTER, R.D., M.A. JENKINS AND A.L. GASKI. 1987. Working bibliography of the peregrine falcon. Natl. Wildl. Fed. Sci. Tech. Ser. 9. Washington, DC U.S.A.

REAL, J. 1991. L'Aliga Perdiguera *Hieraaetus fasciatus* a Catalunya: status, ecología trófica, biología reproductora i demografía. Ph.D. dissertation, Univ. Barcelona, Barcelona, Spain.

RESTANI, M. 1991. Resource partitioning among three *Buteo* species in the Centennial Valley, Montana. *Condor* 93:1007–1010.

REYNOLDS, R.T. AND E.C. MESLOW. 1984. Partitioning of food and niche characteristics of coexisting *Accipiter* during breeding. *Auk* 101:761–779.

SIMMONS, R.E., D.M. AVERY AND G. AVERY. 1991. Biases in diets determined from pellets and remains: correction factors for a mammal and bird-eating raptor. *J. Raptor Res.* 25:63–67.

TELLA, J.L. 1991. Estudio preliminar de la alimentación del alimoche (*Neophron percnopterus*) en el Valle medio del Ebro. Cong. Int. Aves Carroñeras (ICONA Ed.): 53–68.

———. 1993. Polyandrous trios in a population of Egyptian vultures (*Neophron percnopterus*). *J. Raptor Res.* 27: 119–120.

——— AND I. TORRE. 1990. Observaciones sobre relaciones cleptoparasitarias interespecíficas en el alimoche *Neophron percnopterus. Butll. GCA* 7:33–35.

THIOLLAY, J.M. 1982. Les resources alimentaires, facteur limitant la réproduction d'une population insulaire de faucons pelerins, *Falco peregrinus brooker Alauda* 50:16–44.

UNDERHILL-DAY, J.C. 1993. The foods and feeding rates of Montagu's harriers *Circus pygargus* breeding in arable farmland. *Bird Study* 40:74–80.

WARD, F.P. AND R.C. LAYBOURNE. 1985. A difference in prey selection by adult and inmature peregrine falcons during autumn migration. *ICBP Tech. Publ.* 5· 303–309.

ZAR, J.H. 1984. Biostatistical analysis. Prentice Hall, Princeton, NJ U.S.A.

COOPERATIVE NESTING BY A TRIO OF BALD EAGLES

DAVID K. GARCELON, GARY L. SLATER,[1] AND CHRISTOPHER D. DANILSON[2]
Institute for Wildlife Studies, P.O. Box 1104, Arcata, CA 95521 U.S.A.

ROGER C. HELM
U.S. Fish and Wildlife Service, Region 1, 911 N.E. 11th Avenue, Portland, OR 97232 U.S.A.

Helpers at the nest have been reported in at least 222 bird species and are widespread taxonomically (Skutch 1961, Grimes 1976, Rowley 1976, Zahavi 1976). Although rare among raptors, helping occurs regularly at nests of the cooperatively breeding Harris' hawk (*Parabuteo unicinctus*; Mader 1975) and Galápagos hawk (*Buteo galapagoensis*; Faaborg 1986). Helpers at the nests of raptors not considered to be cooperative breeders have been reported for the peregrine falcon (*Falco peregrinus*; Spofford 1969), red-tailed hawk (*Buteo jamaicensis*; Wiley 1975), merlin (*Falco columbarius*; James and Oliphant 1986),

Mississippi kite (*Ictinia mississippiensis*; Parker and Ports 1982), American kestrel (*Falco sparverius*; Wegner 1976), and Eurasian sparrowhawk (*Accipiter nisus*; Newton 1973)

Bald eagles (*Haliaeetus leucocephalus*) are monogamous and highly territorial (Stalmaster 1987). Sherrod et al. (1977) observed three adult bald eagles at two nests on Amchitka Island, Alaska, and Fraser et al. (1983) did so for a nest in Minnesota. Neither, however, presented details on the involvement of the third adult. In this paper we describe a trio of bald eagles that cooperated in territory defense, incubation and the provisioning of nestlings through fledging.

STUDY AREA AND METHODS

In 1980 a program was initiated to reestablish breeding bald eagles onto Santa Catalina Island, where the species was extirpated by the early 1960s (Garcelon 1988). The island is approximately 194 km² and is located 34 km southwest of Long Beach, California. Because residual DDE compounds remained in the environment (Garcelon et al. 1989), nesting attempts early in the program failed,

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[1] Present address: Department of Wildlife and Range Sciences, University of Florida, Gainesville, FL 32751 U.S.A.
[2] Present address: Department of Biology, Boise State University, Boise, ID 83725 U.S.A.

Table 1. Participation by adults in nesting activities at three bald eagle nests in 1992 on Santa Catalina Island, California. One territory consisted of a trio of adults and the other two each consisted of a pair. N = total number of times each activity was observed at each nest.

| | TRIO NEST | | | | PAIR A | | | PAIR B | | |
ACTIVITY	% MALE	% FEMALE	% HELPER	(N)	% MALE	% FEMALE	(N)	% MALE	% FEMALE	(N)
Prey delivery	67	16	17	(77)	68	32	(74)	58	42	(33)
Feeding eaglet	22	45	33	(117)	26	74	(94)	6	94	(69)
Nest material delivery	17	34	46	(67)	45	55	(38)	20	80	(20)

and the manipulation of eggs and the fostering of nestlings were initiated.

In 1991, two eggs were removed from a nest at the northwest end of the island and replaced with a viable egg. During the incubation period a third adult attempted to enter the territory on several occasions, but was driven off by a member of the nesting pair. The intruder was seldom seen in the territory after the egg hatched. In January 1992, a video camera was placed near the nest to document egg-laying times and identify prey items.

The three adults were identified by the following characteristics: (1) one eyelid of the paired female was closed because of an injury suffered during the 1992 breeding season, (2) the third eagle was smaller than the paired female, and (3) the paired male was the smallest of the three birds, and was banded on the opposite leg from the other birds. Although sex was known for all eagles released on the island, the third eagle was not color-marked and we were unable to determine its sex or age. On 24 March the clutch was taken for captive incubation and replaced with dummy eggs.

OBSERVATIONS

Three adult eagles were seen simultaneously in the area prior to egg laying, and on 15 March 1992, the mated pair laid the first of two eggs. On 20 April, the third eagle was confirmed to be participating in incubation. Problems with the video-monitoring system prevented determining the percentage of time the helper incubated.

On 2 May, we placed a foster eaglet approximately 2-wk-old in the nest. All three adults participated in brooding, feeding, and procuring food for the eaglet. On a few occasions all three adults were observed either standing or lying in the nest with the eaglet. On five occasions the helper and mated female were observed feeding the eaglet simultaneously, and in one instance the mated female tore food from a prey item, and relinquished it to the helper which then fed the eaglet. During four other feeding bouts the helper appeared to steal food from the beak of the mated female, and then either consumed it or fed it to the eaglet.

Based on comparisons with adult birds at two other active nests on Santa Catalina Island, our observations indicate that the paired female at the trio nest derived a greater energetic benefit from the presence of the helper than did the male (Table 1). For example, although adult males at all three nests made similar percentages of prey deliveries, the mated female at the trio nest procured food only half as often as the females at the other two nests (Table 1).

On 15 June, we visited the trio nest to band and equip the eaglet with a radio-telemetry transmitter. All three adults aggressively defended the nest while researchers were in the area. On 16 or 17 July the nestling fledged, and the three adults were still in the territory on 9 September when observations ended. Although a considerably smaller amount of time was spent observing this nest in 1993 and 1994, a trio of adult eagles was present at this nest each year during the entire breeding season, and they reared a fostered nestling on each occasion.

DISCUSSION

If the helper bird was a female, as suspected because of its size compared to the adult pair, helping behavior may have been driven by a lack of available mates. Skewed sex ratios have been suggested to lead to cooperative breeding in certain species (Emlen 1978, Faaborg et al. 1980, Reyer 1980) as has habitat saturation (Woolfenden and Fitzpatrick 1984). During the three breeding seasons when a trio of bald eagles nested cooperatively, only 8–11 adult birds were known to be on the island, and four of these were unpaired adult females. In addition, the closest breeding population of bald eagles (more than one pair) was more than 650 km from the island; thus, no alternative breeding areas or mates were readily available.

Trivers (1972) and Maynard-Smith (1977) postulated that for an animal to maximize its inclusive fitness it should regulate its investment in offspring relative to expected costs and benefits. Among other factors, the coefficient of relatedness to the young it rears can determine the benefit a helper will receive in terms of its fitness (Reyer 1984). While helpers are generally related to the breeding pair that they are assisting (Skutch 1987), this is not always the case (Rood 1978, Reyer 1984).

If inclusive fitness is excluded as the potential benefit for the helper at the Catalina Island eagle territory (assuming the helper did not lay one of the two eggs), other possible benefits such as gaining breeding experience or inheriting a breeding territory (Woolfenden and Fitzpatrick 1984) might have been the reward. It is extremely unlikely the helper eagle on Catalina Island gained an inclusive fitness benefit from tending the eggs and eaglet, given that all eagles present on the island were originally

removed as nestlings from different nests located throughout the Pacific Northwest.

If the male eagle of a pair does not have to forage to support the helper, and the helper cares for the egg and nestling, defends the territory, and assists in procuring food, then it is beneficial for the male to allow the presence of the helper. Also, in some species where helpers are common, productivity at nests with helpers is generally higher compared to nests without helpers (Woolfenden 1975, Reyer 1980, Rabenold 1984).

RESUMEN.—En 1992, fue encontrado un territorio de *Haliaeetus leucocephalus* en Santa Catalina Island, California, con tres adultos presentes en un nido. Desde 1992 hasta 1994, la pareja consorte y un ayudante (probable hembra participaron en la incubación de los huevos, empollamiento, alimentación del polluelo y obtención de alimentos. La asistencia de un ayudante en el nido, permite gastar menos tiempo a la pareja en obtener presas y alimentar a los polluelos, en camparación con dos nidos y con una sola pareja de adultos en cada uno.

[Traducción de Ivan Lazo]

LITERATURE CITED

EMLEN, S.T. 1978. The evolution of cooperative breeding in birds. Pages 245–281 *in* J.R. Krebs and N.B. Davies [EDS.], Behavioral ecology, an evolutionary approach. Blackwell Scientific Publ., Oxford, U.K.

FAABORG, J. 1986. Reproductive success and survivorship of the Galápagos hawk *Buteo galapagoensis*: potential costs and benefits of cooperative polyandry. *Ibis* 128:337–347.

———, T. DE VRIES, C.B. PATTERSON AND C.R. GRIFFIN. 1980. Preliminary observations of the occurrence and evolution of polyandry in the Galápagos hawk (*Buteo galapagoensis*). *Auk* 97:581–590.

FRASER, J.D., L.D. FRENZEL, J.E. MATHISEN AND M.E. SHOUGH. 1983. Three adult bald eagles at an active nest. *Raptor Res.* 17:29–30.

GARCELON, D.K. 1988. Reintroduction of bald eagles to Santa Catalina Island, California. M.S. thesis, Humboldt State Univ., Arcata, CA U.S.A.

———, R.W. RISEBROUGH, W.M. JARMAN, A.B. CHARTRAND AND E.E. LITTREL. 1989. Accumulation of DDE by bald eagles reintroduced to Santa Catalina Island in Southern California. Pages 491–494 *in* B.-U.

Meyburg and R.D. Chancellor [EDS.], Raptors in the modern world. World working group on birds of prey and owls, Berlin, Germany.

GRIMES, L.G. 1976. The occurrence of cooperative breeding behavior in African birds. *Ostrich* 47:1–15.

JAMES, P.C. AND L.W. OLIPHANT. 1986. Extra birds and helpers at the nests of Richardson's merlin. *Condor* 88:533–534.

MADER, W.J. 1975. Extra adults at Harris' hawk nests *Condor* 77:482–485.

MAYNARD-SMITH, J. 1977. Parental investment: a prospective analysis. *Anim. Behav.* 25:1–9.

NEWTON, I. 1973. Studies of sparrowhawks. *Br. Birds* 66:271–278.

PARKER, J.W. AND M. PORTS. 1982. Helping at the nest by yearling Mississippi kites. *Raptor Res.* 16:14–17.

RABENOLD, K. 1984. Cooperative enhancement of reproductive success in tropical wren societies. *Ecology* 65:871–885.

REYER, H.-U. 1980. Flexible helper structure as an ecological adaptation in the pied kingfisher (*Ceryle rudis rudis* L.). *Behav. Ecol. Sociobiol.* 6:219–227.

———. 1984. Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). *Anim. Behav.* 32:1163–1178.

ROOD, J.P. 1978. Dwarf mongoose helpers at the den. *Z. Tierpsychol.* 48:277–287.

ROWLEY, I. 1976. Co-operative breeding in Australian birds. Pages 657–666 *in* H.J. Frith and J.H. Calaby [EDS.], Proc. XVI Intern. Ornithol. Congr. Australian Acad. Sci., Canberra, Australia.

SHERROD, S.K., C.M. WHITE AND F.S.L. WILLIAMSON. 1977. Biology of the bald eagle on Amchitka Island, Alaska. *Living Bird* 15:143–182.

SKUTCH, A.F. 1961. Helpers among birds. *Condor* 63. 198–226.

———. 1987. Helpers at bird's nests: a worldwide survey of cooperative breeding and related behavior. Univ. Iowa Press, Iowa City, IA U.S.A.

SPOFFORD, W.R. 1969. Extra female at a nesting site. Pages 418–419 *in* J.J. Hickey [ED.], Peregrine falcon populations: their biology and decline. Univ. Wisconsin Press, Madison, WI U.S.A.

STALMASTER, M.V. 1987. The bald eagle. Universe Books, New York, NY U.S.A.

TRIVERS, R.L. 1972. Parental investment and sexual selection. Pages 136–179 *in* B. Campbell [ED.] Sexual selection and the descent of man. Aldine Press, Chicago, IL U.S.A.

WEGNER, W.A. 1976. Extra-parental assistance by male American kestrel. *Wilson Bull.* 88:670.

WILEY, J.W. 1975. Three adult red-tailed hawks tending a nest. *Condor* 77:480–482.

WOOLFENDEN, G.E. 1975. Florida scrub jay helpers at the nest. *Auk* 92:1–15.

——— AND J.W. FITZPATRICK. 1984. The Florida scrub

jay: demography of a cooperative-breeding bird. Princeton Univ. Press, Princeton, NJ U.S.A.

ZAHAVI, A. 1976. Co-operative nesting in Eurasian birds. Pages 685–693 *in* H.J. Frith and J.H. Calaby [EDS.], Proc. XVI Intern. Ornithol. Congr. Australian Acad. Sci., Canberra, Australia.

LETTER

ATTACKS ON LIVESTOCK BY EURASIAN GRIFFONS IN NORTHERN SPAIN

The Eurasian griffon (*Gyps fulvus*) is the most abundant of four species of vultures inhabiting the Iberian Peninsula Its populations have greatly increased there from 1979–89 (B. Arroyo, E. Ferreiro and V. Garza 1990, II censo nacional de buitre leonado (*Gyps fulvus*). Población, distribución, demografía y conservación. ICONA, Madrid, Spain). Griffon vultures are scavengers that feed on medium- and large-sized carcasses of domestic livestock. However, D.C Houston (1974, Food searching in griffon vultures. *E. Afr. Wildl. J.* 12:63–77), S. Cramp and K.E.L. Simmons (1980, The birds of the western Palearctic, Oxford Univ. Press. Oxford, U.K.), and P. Mundy et al. (1992, The vultures of Africa. Academic Press, London, U.K.) have pointed out that griffons can sometimes kill animals that are too sick or weak to protect themselves. This paper describes an observation of Eurasian griffons preying on a live sheep in La Rioja (northern Spain), and compiles information about similar cases in neighboring regions of Navarra and the Basque country.

In the late afternoon (1955 H) of 23 August 1989 in La Rioja, two hooded crows (*Corvus corone*) were seen pecking at the back of an unmoving recumbent sheep. About ten griffons stood nearby observing the crows. Suddenly the ewe got up and the crows and vultures fled. On examination of the ewe we saw that crows had pecked out one eye. Before dawn the next morning the ewe was still alive, lying with head up facing a group of about 90 vultures. A.C. watched the vultures with a 20–60× telescope until 1230 H at which time a vulture approached the ewe and pecked fleece from its back. Suddenly the mass of vultures approached and started to feed on the ewe. The ewe was very old, suffered from stagger (*Cenurus cerebralis*), and would have died in the next few days. Similar observations on predation by other griffon species have been made by A.F. Boshoff (1989, More on the cape vulture-livestock controversy. *Vulture News* 21:20–21), A. Pringle (1990, cape vultures feeding on a live cow. *Witwatersrand Bird Club News* 150:10), and P. Mundy et al. (1992, The vultures of Africa. Academic Press, London, U.K.)

We have also witnessed evidence of attacks on ewes while lambing and on newborn lambs. Ewes were found with wounds on the vulva and anus that were certified by veterinarians to be evidence that these attacks occurred. At least 5–10 attacks per year were estimated. J.L. Tellería and E. de Juana (pers. comm.) saw vultures waiting close to, but not attacking, ewes giving birth both in Navarra and Cadiz provinces.

A common practice for carrying ewes among Spanish shepherds is to tie the feet together with a rope. Both in La Rioja and in the Basque country, ewes thus tethered were preyed upon by griffons. In the latter area shepherds came upon vultures feeding on six ewes. One of the sheep had to be sacrificed and the rest died during the following days.

We think that predation by griffons occurs under famine conditions and not when food is abundant. In La Rioja, where A.C. has carried out studies on griffons since 1985, food availability has remained at about the same level over the last 9 yr. Nevertheless, it should be considered that predation by griffons is an occasional way of obtaining food.—
Alvaro Camiña Cardenal, C/Cristóbal Colón 6 2° izda, Guecho, Vizcaya, Spain, Alejandro Honrubia Baticon, C/Francisco Suárez 2° C, 2° D, 47006 Valladolid, Spain, and Alfonso Senosiain, C/ Goroabe 21 bajo, 31005 Pamplona, Spain.

BOOK REVIEWS

EDITED BY JEFFREY S. MARKS

The Eastern Screech Owl: Life History, Ecology, and Behavior in the Suburbs and Countryside. By Frederick R. Gehlbach. 1994. Texas A & M University Press, College Station, TX. xiv + 302 pp., color frontispiece, 36 black-and-white photos, 23 figures, 27 tables, 10 appendices. ISBN 0-89096-609-5. Cloth, $45.00.—Many species of birds, including several species of raptors, regularly occupy human-altered habitats in cities and suburbs. Most of these species also occur in more natural habitats. Because urbanization continues at a rapid pace, it is certainly relevant to ask how the behavior and ecology (and, specifically, reproductive rates) of birds in urban areas compare with those of birds in more natural areas. Unfortunately, few investigators have attempted to answer these questions. The objective of Gehlbach's study was to do just that for the eastern screech-owl (*Otus asio*) or, in his words, "to estimate what is needed for the bird's successful coexistence with humanity." This book is based on his work with these owls over a 25-yr period in central Texas.

Each chapter begins with a brief personal note, and all but the last chapter end with a summary. Chapter 1 ("On Studying Screech Owls") describes a 9-yr "exploratory period" during which the author monitored nine nest boxes in suburban Waco attempting "to learn by trial and error, eliminate mistakes, and formulate hypotheses based on personal experience." The study areas and general methods used during the 16-yr "confirmatory study" that followed are also described, along with statistical tests used to analyze the data. Chapter 2 ("Landscapes") contains more information about the study areas and describes nest- and roost-site selection by the owls. Prey use and predatory tactics are discussed in Chapter 3 ("Food Supplies and Predation"). Basic life-history information is presented in Chapters 4 ("Adult Weight, Coloration, and Molt"), 5 ("Eggs and Incubation"), 6 ("Chicks and Fledglings"), and 7 ("Vocalizations"). Factors contributing to lifetime reproductive success are examined in Chapter 8

("Lifetime Reproduction"), whereas survival, productivity, and use of space are examined in Chapter 9 ("Population Structure and Flux"). Chapter 10 ("The Suburban Advantage") summarizes why eastern screech-owls do well in suburbia and provides methodological hints for those who might wish to initiate similar studies of screech-owls. Among the 10 appendices, one includes 24 pages of paraphrased field notes, another summarizes the development of two nestlings raised in captivity, and others provide information about climate, habitat features, cached foods, food availability based on surveys of terrestrial vertebrates, species that mobbed screech-owls, lifetime reproduction, life tables, and scientific names used in the text. The notes section is used primarily to cite references but also to provide "further descriptive details and occasional ancillary observations."

This book contains a wealth of information about the breeding biology of eastern screech-owls. For example, there are valuable data on laying intervals, clutch sizes, duration of incubation and brooding periods, nestling growth rates, nestling survival rates, differences between first nests and replacement nests, and factors that influence productivity and lifetime reproductive success. The different roles played by males and females in reproduction are described clearly. Information is also provided about the relationship between mobbers and "mobbees," body mass dynamics, and the nest-cavity symbiosis between screech-owls and Texas blind snakes (*Leptotyphlops dulcis*). Other notable contributions are the discussions of caching behavior (although see below) and the general descriptions of vocalizations and vocal behavior (although no sonagrams are provided).

As the book's title suggests, a major objective was to compare the ecology of suburban and rural screech-owls. Gehlbach monitored both groups over a 12-yr period and found that suburban owls occurred at higher densities and had greater reproductive success than those in the rural study area (located 7 km from the primary suburban study area). Suburbia may offer several advantages, including a milder climate (because of the urban "heat island" effect), higher

prey densities, and a relatively open habitat that may make for easier hunting. More importantly, suburbia may have fewer competitors and predators, and human activity near owl nests probably deters those predators that are present. In fact, data revealed that "rural owls had as much potential per prospective breeder, but predation just overwhelmed them" (p. 173).

The book did have some weaknesses. There were at least 19 typographic errors, and I disliked one aspect of the book's format. Literature citations plus additional comments were placed in a notes section at the end of the book. I found this arrangement to be inconvenient and would have preferred to have much of this material incorporated into the text. More importantly, Gehlbach sometimes failed to provide sufficient detail concerning statistical tests and methods used in gathering the data. This criticism might not be completely fair because Gehlbach points out (p. xi) that he has written "a personal narrative, so the story might be of interest to all . . . ." However, he also points out that "I include quantitative detail sufficient to be relevant to ecologists and ornithologists." In several cases, I believe Gehlbach failed to do so. Although a summary of statistical methods is provided in Chapter 1, Gehlbach sometimes presents P values with no indication of the test used and no clear mention of sample sizes. For example, "Flights in open and wooded yards did not differ either but were longer than the 17-m average hunting flights of the boreal owl ($P = 0.05$)" (p. 53).

A cursory description of methods is provided in Chapter 1, but important details are sometimes omitted. For example, Gehlbach indicates that most owls were sexed by body mass (p. 65), but he does not provide the cutoff point separating males from females. In contrast, Smith and Wiemeyer (1992) cautioned against using mass to sex eastern screech-owls. A discriminant function analysis based on body mass plus wing and tail length correctly identified the sex of just 88% of 77 individuals (Smith and Wiemeyer 1992), yet Gehlbach suggests that mass alone can be used to determine sex.

Details about observational procedures are sometimes omitted. For example, Gehlbach notes (p. 81) that females remained inside nest cavities for an average of 5.7 d before laying. However, he did not indicate how this was determined. Did he or his assistants maintain constant watch? If not, how often were the cavities or boxes checked to determine the

location of the females? Gehlbach also asserts (p. 58) that food deliveries to nests by adults exhibited a distinctly bimodal distribution, with the major peak at dusk. Elsewhere, however, he indicates (p. 13) that nighttime observations typically were made from "sunset to around 2200 H and near dawn for an hour or two." Were observations sometimes extended through the night so that patterns of food delivery could be discerned? Similarly, Gehlbach reports data for rodent and snake populations in the "perimeter zone" but not in the suburban plot because "short-term exploratory trapping and rock-turning in suburbia suggested that there were no profound differences." Unfortunately, there is no indication of how "short-term" the trapping was nor what constitutes a "profound" difference. Thus, for reasons that are not clearly explained, rodent populations were estimated by trapping in a tallgrass prairie remnant on the southern edge of his perimeter zone 2 km south of the primary suburban study area. Concerning bird populations, Gehlbach monitored a 6.1-ha plot in the primary suburban study area and indicated (pp. 39–40) that "the birds of this area were trapped, netted, banded, and marked on a map weekly, November to June, 1976–91." He also "mapped all birds" in a 6.1-ha rural plot from 1976–91. Unfortunately, no details are provided; e.g., no indication of how much time was spent in each plot each week. Further, mapping as a census technique does not work well on birds that are not territorial and so is typically used only during the breeding season (Bibby et al. 1992). Despite this, Gehlbach apparently "mapped" birds in his rural plot even during the nonbreeding season.

As another example, vocalizations given by adults at nest sites, and differences between the vocal behavior of males and females, are described, but it is not clear how and when the data were collected. In the first chapter, Gehlbach points out (p. 13) that when making observations at nest sites he would typically "sit against a tree or house about 15 m from their nests." Were all observations of vocal behavior made under such conditions, or were nests sometimes approached more closely? The use of "screech" calls by the owls suggests closer approaches (Sproat and Ritchison 1994).

I would also have liked more information concerning how roosting screech-owls were located (p. 32). Because the owls were not radiotagged, was there a bias toward finding owls in lower, more open roosts? Gehlbach presents much information about

caching behavior but does not describe clearly how these data were gathered. Were all boxes and nest cavities checked daily? On p. 39, he does note that "in only eight percent of 152 larders, which I checked daily . . . " did the owls fail to eat what they had stored. That suggests to me that once a cached item was located, he checked daily to determine its fate. However, there is no information concerning when or how frequently nest boxes and cavities were checked for cached items.

Additional detail about Gehlbach's experiments with radiotransmitters would also have been useful because at three points in the book (pp. 131, 177, and 267) he uses these results to explain differences between his findings and those of other investigators. Gehlbach tried radiotelemetry with two males and reported that, compared with untagged owls, these males lost more weight and moved more often over a wider area. Unfortunately, no mention is made of either the weight of the transmitters or the body mass of the owls that were radiotagged. Further, neither the extent of mass loss nor the movement data are quantified.

Sample sizes or the number of individual owls observed are sometimes not provided (or are not apparent), and sometimes data are simply not presented. For example, concerning winter roosting behavior, Gehlbach points out (p. 34) that "when one sex was present, the other was usually in the nearest cavity ($r_s = 0.77$, $P = 0.001$)." However, no indication is given of how many pairs were observed or how many observations were made of each pair. On the same page, it is noted that 64.7 ± 8.7% of male screech-owls used their winter-roost boxes for nesting, but again the sample size is not provided. Gehlbach reports (p. 56) that 11 suburban males entered their nest-box roosts an average of 18.7 min before sunrise in December to February. Was this based on one observation per male? Gehlbach found roosting owls on 293 occasions (p. 32). Does this represent 293 different owls, or were some birds observed roosting on more than one occasion? Similarly, 165 hunting forays were observed (p. 39). Were some hunting owls observed more than once? On p. 129, it is reported that "males sometimes attacked me as I climbed to fourth-week nestlings . . . but females did so almost invariably." How many pairs were observed and how many "trials" conducted? On p. 130, Gehlbach notes that 3–4 wk after fledging, owlets "traveled up to 200 m per night but tended to remain together inside parental ranges" and, fur-

ther, that adults "often" chased owlets during natal dispersal. No supporting data are provided. On p. 143, it is suggested, concerning nest defense, that "the larger the predator or other interloper, the bolder its actions, and the more novel or sudden its appearance, the more likely owls are to screech." Once again, however, there are no supporting data.

There were other occasions when I would have liked additional information. Gehlbach points out that individual nesting territories consist of isolated patches around nest sites (boxes or cavities), with males typically defending two or three sites per season but, apparently, not defending the areas between the sites. Such behavior is very different from that exhibited by eastern screech-owls elsewhere (e.g., Kentucky; Belthoff et al. 1993), and information concerning the frequency with which other males used those areas between the defended nest sites (or, using the terminology of Gehlbach, polyterritories) would have been of great interest. Another rather novel suggestion was that female screech-owls temporarily leave their mates during the winter to reduce intraspecific competition for food (p. 36). How was it determined that females had left? Was it assumed that females not found roosting in particular nest boxes or natural cavities had left their mates? Gehlbach notes that the few females located away from defended nest sites were within 0.5 km of their mates but provides no additional information. What was the average distance from mates? How far were the females from the edges of their mates' ranges? Is it possible that the ranges of females and their mates overlapped and, therefore, that females were not actually leaving their mates? In this case, radiotelemetry might have provided much useful information.

As the preceding paragraphs suggest, I liked some aspects of the book but disliked others. On the positive side, there is an abundance of information about the breeding biology of eastern screech-owls and, more precisely, about the comparative behavior and ecology of screech-owls in suburban and rural areas. On the negative side, however, some of these data (and, therefore, some of Gehlbach's conclusions) are, in my opinion, of questionable value because insufficient detail is provided about how the data were collected. As mentioned above, this book represents an attempt by the author to write a story "of interest to all." Unfortunately, Gehlbach has probably included more quantitative detail than many nonbiologists would like but less such detail than most

biologists would require. Although these negatives reduce the value of this book, it should be read by anyone interested in owls (particularly their breeding biology) and, more generally, by anyone interested in finding out how at least one species manages to coexist with humans.—**Gary Ritchison, Department of Biological Sciences, Eastern Kentucky University, Richmond, KY 40475 U.S.A.**

LITERATURE CITED

BELTHOFF, J.R., E.J. SPARKS AND G. RITCHISON. 1993. Home ranges of adult and juvenile eastern screech-owls: size, seasonal variation and extent of overlap. *J. Raptor Res.* 27:8–15.

BIBBY, C.J., N.D. BURGESS AND D.A. HILL. 1992. Bird census techniques. Academic Press, San Diego, CA U.S.A.

SMITH, D.G. AND S.N. WIEMEYER. 1992. Determining sex of eastern screech-owls using discriminant function analysis. *J. Raptor Res.* 26:24–26.

SPROAT, T.M. AND G. RITCHISON. 1994. The antipredator vocalizations of adult eastern screech-owls. *J. Raptor Res.* 28:93–99.

The Wisdom of the Spotted Owl: Policy Lessons for a New Century. By Steven Lewis Yaffee. 1994. Island Press, Washington, DC. xxviii + 430 pp., 2 tables. ISBN 1-55963-203-8. Cloth, $45.00; paper, $26.95.—The intention of the author was not to write a book about the biology and natural history of the spotted owl (*Strix occidentalis*), but to use the controversy surrounding this species as a vehicle for exploring larger issues concerning resource management in North America. To accomplish this task, he drew on historical documents, internal agency correspondence, agency plans, governmental proceedings, and interviews with key people involved with the issue. Sources of information are catalogued in 34 pages of footnotes at the end of the book.

At the outset, the title is somewhat misleading in that the book deals solely with the northern spotted owl (*S. o. caurina*) and not with the California (*S. o. occidentalis*) or Mexican (*S. o. lucida*) subspecies, each of which is embroiled in its own controversies. As such, the book focuses on management practices for public lands in the Pacific Northwest, primarily Oregon and Washington. As the principal land management agency in this region, the U.S. Forest Service (USFS) receives the most attention, with the roles of the Bureau of Land Management (BLM), U.S. Fish and Wildlife Service (USFWS), and various state agencies being treated more superficially. The book includes a brief introduction followed by three major parts: "The Evolution of the Spotted Owl Controversy" (Part I), "Learning from History" (Part II), and "Policy Implementations for the 1990s and Beyond" (Part III). The introduction sets the tone for the remainder of the book and provides a useful overview of each chapter within the major parts.

"The Evolution of the Spotted Owl Controversy" details the separate paths taken by resource agency policies and changing public values from which the northern spotted owl controversy arose. Chapter 1 ("Birth of a Controversy: 1945–1977") describes early management policies and philosophies of the USFS. These center around resource extraction (principally logging) as it coincided with the country's current values and how the agency failed to adequately accommodate the increasing environmental, aesthetic, and recreational values of people using forests in the early 1970s and beyond. This chapter also details some of the early research on spotted owls in Oregon and its impact on the development of management plans by the Oregon Endangered Species Task Force (OESTF). The second chapter ("Muddling Through: 1978–1981") discusses responses by the USFS and BLM to the initial OESTF plan and how these agencies behaved given the management philosophies inherited from previous decades. At this point, both environmental and timber industry groups entered the stage, and the issue became increasingly polarized. In these first two chapters, Yaffee uses excerpts from interviews with biologists and land planners and correspondence among agency officials to provide strong examples of how the controversy that ensued could have been forestalled with more visionary leadership by agency officials presented with a growing body of research on spotted owls. Chapters 3 ("New Science, New Directives, More Muddling: 1981–1984") and 4 ("The Forest Service's Last Stand: 1985–1989") outline attempts by the USFS and BLM to develop formal management plans that would satisfy demands by both environmental groups and the timber industry in the face of the growing controversy. Again, extensive excerpts from interviews and correspondence provide an insider's view into the issue

and give a personal perspective of the pressures being exerted on agency personnel from outside influences as well as from within their own agencies. Yaffee also provides a glimpse into the back-room planning process, the discussions involved, and some of the personalities involved. At this point, lawsuits by both environmental and industry groups against the USFS and BLM began to escalate, and the possibility of listing the owl under the Endangered Species Act was imminent. However, these are discussed in less detail than I would have liked. Yaffee continues on the track of emphasizing the role of the USFS above all others. The last chapter of Part I ("All Hell Breaks Loose: 1989–1993") is the weakest. It was during this period that the northern spotted owl was listed as "threatened" under the Endangered Species Act, a joint management plan was developed by the USFS and BLM, a recovery plan was written, and President Clinton attempted to settle the dispute with a much-publicized timber summit. Yaffee only briefly covers the problems encountered in listing the species. He fails to mention that one of the early status reviews was doctored by upper administrative officials of the USFWS, and that the draft recovery plan was never adopted. In addition, he fails to mention that the "God Squad" exemption included only 17 of the 44 sales considered and totaled less than 810 ha of timber (p. 139). There were considerable implications for the Endangered Species Act resulting from the spotted owl controversy that could have been examined in more detail. Yaffee also gives minimal credit to the Interagency Scientific Committee (ISC) plan; most biologists (including myself) felt it was the most scientifically credible plan in existence (see Murphy and Noon 1992). Instead, Yaffee considers an earlier USFS plan (the FSEIS) to be the landmark plan. This plan was short on empirical data but long on dogmatic theory; few biologists felt it was as credible as the ISC plan. Despite these flaws, however, Yaffee provides an informative overview of the time period in question and does an admirable job of pulling together the many-faceted aspects of the controversy that set the stage for the remainder of the book.

Part II ("Learning from History") develops the argument that the controversy surrounding the spotted owl involved more than just the owl itself. Yaffee explores the issue in the broader context of land preservation, political autonomy, log exports, and additional economic factors. In addition, he takes a larger view of the nature and structure of our gov-

ernment and society and how these factors work against immediate and timely solutions. The first chapter of this section (Chapter 6, "Tough Choices: A Difficult Issue Under Any Circumstances") details the economic forces and the different value systems and philosophies among land managers, loggers, and environmentalists that almost guaranteed that no middle ground would be acceptable. Chapter 7 ("Avoiding Tough Choices: American Decisionmaking Processes") explores the structure of land management agencies in relation to each other and the larger administrative framework and how this structure led to political and administrative fragmentation and lack of coherent decisions concerning land management and the spotted owl. Yaffee also discusses our societal propensity toward crisis management and the lack of creativity in resource agencies that might avoid future crisis management situations. One overlooked issue is that of accountability by agency personnel for failure to adequately implement policy. Failure of spotted owl plans stemmed as much from a purposeful failure to follow their intent as from the inadequacies of the plans themselves. Chapter 8 ("Influencing Tough Choices: Actors in American Decisionmaking Processes") examines how individual personalities of key decision makers, media influences on public perceptions, and strategies employed by public interest groups all affect how and when decisions are (or are not) made. Most of the chapter deals with the latter issue and includes interesting examples of how both industry and environmental groups used a variety of tactics to accomplish their respective goals. Yaffee provides in-depth perceptions of the resource agencies, primarily the USFS, in Chapters 9 ("Insufficient Policies and Misleading Politics") and 10 ("Grounded in the Past: Agency Values and Management Approaches"). The latter chapter could as easily have been entitled "The Rise and Fall of the U.S. Forest Service." Overall, these chapters are excellent. Yaffee outlines what the USFS should be, what it once was, and balances that with how resource-based agencies failed in dealing with the spotted owl issue, partly due to their own intransigence and partly due to conflicting societal and legal mandates. For example, the mandate of multiple-use in the USFS worked so long as it did not conflict with consumptive uses. However, conflicts increased as resources became scarcer and values changed, and the USFS was placed in the difficult position of being unable to please everyone all of the time. The agency's inability

to adapt to a changing society only compounded the problem. In general, Part II switched between dogmatic presentation of the author's opinions to what I felt were well-documented interpretations of the situation. Overall, I think Dr. Yaffee introduced perceptive and objective analyses of the situation from different angles, such as how people with disparate values interact with each other and at different scales progressing from the impact of individuals to small interest groups to larger governmental entities.

In Part III ("Policy Implications for the 1990s and Beyond"), Yaffee attempts to use history as a lesson for preventing future mistakes in resource management. The first chapter (11, "The Context for Change") begins by using results from various surveys to examine the backdrop of our society; i.e., how we feel about environmental issues, our relationship with our government, and our value structure. This chapter continues by describing the increased systemic stress on our public lands and the resources contained therein, the lack of fiscal resources to deal with this generalized problem, and the rising influence of competing political action committees. This section provides a multitude of information on public attitudes and federal funding that Yaffee uses to build the case that, while citizens want resource protection, this ambition has not been matched by appropriate levels of funding. The chapter ends on a positive note by examining a number of reasons for being optimistic about resolution of future problems and ways in which the spotted owl issue may have positively influenced how natural resource conflicts will be dealt with in the future. The last two chapters of the book (12, Building More Effective Agencies and Decisionmaking Processes" and 13, "Building Better Policies") discuss how natural resource agencies can better deal with conflicts. Yaffee does not just criticize, he also offers solutions, some of them quite detailed. Again, the USFS serves as the model for most of the suggestions, although they have broader applicability to other organizations. Yaffee makes suggestions at different operational levels ranging from personnel in the field to upper management levels. His most useful discussions concern changes in the way the USFS, as a whole, should do business, moving from a "quasi-industrial, military style" to "science-based and concurrence-seeking." The final chapter places the issue of public land management in the larger picture, suggesting changes in land classification, the role of

subsidies, regional planning, and public and academic involvement. These two chapters would have been better served by additional interviews with agency personnel as to what their perceptions for improvement are and whether Yaffee's suggestions are feasible.

For the most part, the book is very well written. Dr. Yaffee attempts to remain an impartial observer and performs this task well. He avoids pointing the sole finger of blame at any one person or organization and instead spreads blame over a number of sources. He looks for the disparate sources of problems, identifies them, and then offers solutions. A major failure of the book, in my view, is the treatment of the role of science and scientists. I felt that Yaffee's understanding of the scientific basis for management of spotted owls is limited and, in some areas, inaccurate. His discussion in Chapter 6 of the role of science (pp. 170–177) lacks an understanding of the importance of various aspects of spotted owl ecology. Moreover, it misses the point that, despite uncertainties, toward the end of the planning process more was known about spotted owls than any other nongame species in North America. Yaffee's limited understanding of the role of science was probably a result of lack of interviews with a number of key scientists. In his emphasis on the USFS, he also neglects the distinction between the research and management branches of that agency and the differences in styles and values between the two branches. Statements such as "Even though the ISC was only partly FS researchers, creation of the group with the specific set of individuals that were named as its members ensured the outcome at the outset" (p. 272) suggest an ignorance of the independent nature of scientists from the research branch of the USFS and their often outspoken criticism of USFS management policy when it contradicts scientific results. However, I felt the section entitled "Science and Scientists in the Policy Process" in Chapter 8 was an insightful summary of the role scientists are forced to play in the political arena. His discussion about the role of experts in our society (p. 294) was equally perceptive.

Every book has its strengths and weaknesses, and this book is no exception. However, my rule of thumb in determining the value of a book is whether I learned something and whether the ideas made me think. Steven Yaffee provided both for me. This book should be read by anyone involved in resource management and especially by anyone involved with spe-

cies that are threatened, endangered, or have the potential for being so. Yaffee builds an intricate case study of the spotted owl issue that serves as a valuable lesson for resource and species management in the United States as a whole. Every raptor biologist should read this book because the spotted owl issue started as innocuously as most current raptor studies are now progressing. Working with charismatic species that exist in relatively low densities (e.g., raptors) almost guarantees that conflicts will eventually arise. In order to forestall the same pitfalls that trapped spotted owl researchers, managers, and policy makers, this book offers an excellent set of tools

and ideas to deal with the issue. It should be on the bookshelf of any person who deals with natural resource issues in one form or another.—**Alan B. Franklin, Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO 80523 U.S.A.**

LITERATURE CITED

MURPHY, D.D. AND B.R. NOON. 1992. Integrating scientific methods with habitat conservation planning: reserve design for northern spotted owls. *Ecol. Appl.* 2: 3–17.

The Journal of Raptor Research is distributed quarterly to all current members. Original manuscripts dealing with the biology and conservation of diurnal and nocturnal birds of prey are welcomed from throughout the world, but must be written in English. Submissions can be in the form of research articles, letters to the editor, thesis abstracts and book reviews. Contributors should submit a typewritten original and three copies to the Editor. All submissions must be typewritten and double-spaced on one side of 216 × 278 mm (8½ × 11 in.) or standard international, white, bond paper, with 25 mm (1 in.) margins. The cover page should contain a title, the author's full name(s) and address(es). Name and address should be centered on the cover page. If the current address is different, indicate this via a footnote. A short version of the title, not exceeding 35 characters, should be provided for a running head. An abstract of about 250 words should accompany all research articles on a separate page.

Tables, one to a page, should be double-spaced throughout and be assigned consecutive Arabic numerals. Collect all figure legends on a separate page. Each illustration should be centered on a single page and be no smaller than final size and no larger than twice final size. The name of the author(s) and figure number, assigned consecutively using Arabic numerals, should be penciled on the back of each figure.

Names for birds should follow the A.O.U. Checklist of North American Birds (6th ed., 1983) or another authoritative source for other regions. Subspecific identification should be cited only when pertinent to the material presented. Metric units should be used for all measurements. Use the 24-hour clock (e.g., 0830 H and 2030 H) and "continental" dating (e.g., 1 January 1990).

Refer to a recent issue of the journal for details in format. Explicit instructions and publication policy are outlined in "Information for contributors," *J. Raptor Res.*, Vol. 27(4), and are available from the editor.

1995 ANNUAL MEETING

The Raptor Research Foundation, Inc. 1995 annual meeting will be held on 1–4 November at the Duluth Entertainment and Convention Center in Duluth, Minnesota. Details about the meeting and a call for papers will be mailed to Foundation members in the summer, and can be obtained from Dan Varland, Scientific Program Chairperson, Rayonier, Northwest Forest Resources, 413 8th Street, Hoquiam, WA 98550, (telephone 360 538-4582; FAX 360 532-5426; e-mail Daniel_Varland@RAYNR.CCMAIL.COMPUSERVE.COM), and Gerald Niemi, Local Chairperson, Natural Resources Research Institute, University of Minnesota Duluth, Duluth, MN 55811 (telephone 218 720-4279; e-mail GNIEMI@SAGE.NRRI.UMN.EDU). For information about the associated symposium "A Comparison of Forest Raptor Responses to Forest Management—A Holarctic Perspective," contact Gerald Niemi.

RAPTOR RESEARCH FOUNDATION, INC., AWARDS
Recognition for Significant Contributions[1]

The **Dean Amadon Award** recognizes an individual who has made significant contributions in the field of systematics or distribution of raptors. Contact: **Dr. Clayton White, 161 WIDB, Department of Zoology, Brigham Young University, Provo, UT 84602 U.S.A.** Deadline August 15.

The **Tom Cade Award** recognizes an individual who has made significant advances in the area of captive propagation and reintroduction of raptors. Contact: **Dr. Brian Walton, Predatory Bird Research Group, Lower Quarry, University of California, Santa Cruz, CA 95064 U.S.A.** Deadline: August 15.

The **Fran and Frederick Hamerstrom Award** recognizes an individual who has contributed significantly to the understanding of raptor ecology and natural history. Contact: **Dr. David E. Andersen, Department of Fisheries and Wildlife, 200 Hodson Hall, 1980 Folwell Avenue, University of Minnesota, St. Paul, MN 55108 U.S.A.** Deadline: August 15.

Recognition and Travel Assistance

The **James R. Koplin Travel Award** is given to a student who is the senior author of the paper to be presented at the meeting for which travel funds are requested. Contact: **Dr. Petra Wood, West Virginia Cooperative Fish and Wildlife Research Unit, P.O. Box 6125, Percival Hall, Room 333, Morgantown, WV 26506-6125 U.S.A.** Deadline: established for conference paper abstracts.

The **William C. Andersen Memorial Award** is given to the student who presents the best paper at the annual Raptor Research Foundation Meeting. Contact: **Ms. Laurie Goodrich, Hawk Mountain Sanctuary, Rural Route 2, Box 191, Kempton, PA 19529-9449 U.S.A.** Deadline: Deadline established for meeting paper abstracts.

Grants[2]

The **Stephen R. Tully Memorial Grant** for $500 is given to support research, management and conservation of raptors, especially to students and amateurs with limited access to alternative funding. Contact: **Alan Jenkins, George Miksch Sutton Avian Research Center, Inc., P.O. Box 2007, Bartlesville, OK 74005-2007 U.S.A.** Deadline: September 10.

The **Leslie Brown Memorial Grant** for $500–$1,000 is given to support research and/or the dissemination of information on raptors, especially to individuals carrying out work in Africa. Contact: **Dr. Jeffrey L. Lincer, Sweetwater Environmental Biologists, Inc., 3838 Camino del Rio North, Suite 270, San Diego, CA 92108 U.S.A.** Deadline: September 15.

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[1] Nominations should include: (1) the name, title and address of both nominee and nominator, (2) the names of three persons qualified to evaluate the nominee's scientific contribution, (3) a brief (one page) summary of the scientific contribution of the nominee.

[2] Send 5 copies of a proposal (≤5 pages) describing the applicant's background, study goals and methods, anticipated budget, and other funding.